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CONTRIBUTION TO THE FLORA OF THE NEW HEBRIDES PLANTS COLLECTED BY S. F. KAJEWSKI IN 1928 AND 1929¹

A. GUILLAUMIN

Plate 43 and two text figures

NYCTAGINACEAE

Calpidia excelsa Heimerl in Oesterr. Bot. Zeitschr. LXIII. 284 (1913).

Aneityum: Anelgauhat Bay, common in rain-forest up to 600 m., no. 974 (coll. *J. P. Wilson*), Aug. 1929 (large tree up to 0.60 m. diameter; flowers small, pink; fruit a small round berry).—Already found on Tanna; also Fiji, Society? and Bismarck Islands, New Guinea, Timor and Malaysia.—Vernacular name "Moca."

Cited erroneously from Norfolk Island, Australia and New Zealand by confusion with *C. Brunoniana* Heimerl.

AMARANTACEAE

Achyranthes aspera Linnaeus, Sp. Pl. 204 (1753).

Tanna: Lenakel, common in native gardens, rain-forest, at 150 m., no. 86, March 3, 1928 (plant about 1 m. high, with pretty variegated leaves of pink and brown).—Also New Caledonia, Loyalty Islands, North Australia, Norfolk Island, Fiji, Tonga, Samoa, Cook, Society, Marquesas, Union, Ellice, Mariana and Bismarck Islands and Malaysia.

POLYGONACEAE

Polygonum minus Hudson, Fl. Angl. ed. 1, 148 (1762).

Eromanga: Dillon Bay, common in rain-forest at sea level, no. 339, May 29, 1928 (a plant growing in semi-cleared patches of rain-forest; mixed with Nunpar-lell, Ney-wass and Ne-cit-ersif for medicine for sickness on left side of stomach).—Also New Caledonia, Australia (Queensland, New South Wales, Victoria, Tasmania), Malaysia (Java) and Philippines (Luzon).—Vernacular name "Neta-pea."

¹ Continued from Vol. XIII. 30.

Polygonum subsessile R. Brown, Prodr. Fl. Nov. Holl. 419 (1810).

Eromanga: Dillon Bay, common on banks of creeks and in swampy places at sea level, no. 367, June 5, 1928 (large plant up to 1.25 m. high; flowers white).—Also New Caledonia and Australia (Queensland, New South Wales, Victoria, Tasmania).—Vernacular name "Ukut-ukut."

PIPERACEAE

Piper latifolium Forster f., Fl. Ins. Austr. Prodr. 5 (1786).

Anenityum: Anelgauhat Bay, common in rain-forest at sea level, no. 718, Feb. 9, 1929 (plant up to 2.5 m. high; fruit brown when ripe; this is the wild Kava and is not used for drinking purposes). *Tanna*: Lenakel, common in heavy rain-forest soil at sea-level, no. 3, Feb. 20, 1928 (broad leaved plant about 1.25 m. high; leaves bright green).—*Banks Group*: Vanua Lava, common in rain-forest at sea level, no. 436, July 9, 1928 (plant up to 1.5 m. high; fruit red when ripe).—Already found on Tanna, Efate and Epi; also Society, Tonga and Fiji Islands and in Timor.—Vernacular name "Wild Kava" (under no. 718) and "Wild N'Kava" (under no. 436).

Piper methysticum Forster f., Pl. Esc. 76 (1786).

Tanna: Lenakel; common in rain-forest at 150 m., no. 119, March 6, 1928 (plant 1.5 m. high; the roots make the native intoxicant N'Kava).—Already found on Efate; also New Guinea, Bismarck, Fiji, Society, Tonga, Marquesas and Wallis Islands and Hawaii.—Vernacular name "N'Kava."

Piper miniatum Blume in Verh. Batav. Genotsch. xi. 166 (1826).

Banks Group: Vanua Lava, common in rain-forest at 500 m., no. 463, July 10, 1928 (parasite on rain-forest trees, fruit red when ripe).—Also New Guinea, Moluccas, Malaysia and Philippines.

Peperomia leptostachyoides C. De Candolle in Bull. Herb. Boiss. ser. 2, VIII. 330 (1908).

Eromanga: Dillon Bay, common on rocks in shade of scrub or rain-forest at sea level, no. 359, June 4, 1928 (plant about 7 cm. high; sap of leaf used to make the faces of the natives glossy). *Efate*: Fila Island, Vila, common in rain-forest of sea shore, no. 188, April 14, 1928 (small plant growing on rocks).—Already found in the New Hebrides.—Vernacular name "Nimtoro-orah" under no. 359).

CHLORANTHACEAE

Ascarina lanceolata Hooker f. in Jour. Linn. Soc. i. 127 (1856).

Tanna: Mt. Tokosh Meru, common in rain-forest at 1000 m., no. 152, March 15, 1928 (tree up to 10 m. high). *Anenityum*:

Anelgauhat Bay, common in rain-forest at 360 m., no. 863, March 5, 1929 (small tree up to 9 m. high; flowers yellow; bark brown and fissured).

The plant from Tanna differs from the typical form of the Fiji and Samoa Islands in the larger leaves (up to 10.5 cm. by 4.5 cm.) and the longer petioles (up to 2.5 cm.), while the plant from Aneityum has narrower lanceolate leaves (up to 12 cm. by 3 cm.).

MYRISTICACEAE

Myristica aff. *M. Hollrungii* Warburg.

Banks Group: Vanua Lava, common in rain-forest at sea level, no. 422, July 6, 1928 (tree up to 25 m. high; fruit brown, 4.5 cm. long, 4 cm. diam.)

No *Myristica* had been found in the New Hebrides, though Warburg (Monog. Myrist. p. 486) indicates that *M. subulata* Miq. of the Aru Island and New Guinea might exist perhaps also in the New Hebrides.

MONIMIACEAE

Hedycaria neo-ebudica Guillaumin, sp. nov.

Arbor parva, 10 m. alta, ramis gracilibus glabris, foliis oppositis vel 3-nis atro-viridibus papyraceis oblongis vel oblongo-elongatis (usque ad 16 cm. \times 5.5 cm.) apice acute acuminatis basi obtuse cuneatis vel sub-rotundatis integerrimis utrinque glabris, nervis 7-10-jugis a venis parum distinctis procul a margine arcuatis tenuissimis subtus tantum prominulis, petiolo 2-2.5 cm. longo; inflorescentiae 3-4.5 cm. longae, receptaculo fructifero plano supra puberulo, drupis maturis nigris ovoideis (0.8 cm. \times 0.6 cm.).

Aneityum: Anelgauhat Bay, common in rain-forest at 125 m., no. 811 (typus), Feb. 23, 1929 (small tree up to 9 m. high; leaves dark green; fruit 8 mm. long, 6 mm. in diam., black when ripe). *Eromanga*: Dillon Bay, common in rain-forest at 400 m., no. 322, May 28, 1928 (tree about 8 m. high; fruit 1.25 cm. long, turbinate with blunted point, very scarce).—Vernacular name "Neyar-riverum" (under no. 322).

This new species approaches *H. denticulata* Perk. & Gilg of the Solomon and perhaps the Tonga Islands, but is readily distinguished by the receptacle being pubescent above. The specimen from Eromanga differs from the type in the oval leaves (not exceeding 10 \times 4.5 cm.) with shorter acumen and broader base and in the shorter, 1-2 cm. long petiole.

Hedycarya, sp. nov.?

Tanna: Lenakel, common in rain-forest at 200 m., no. 90, March 5, 1928 (specimens from tree about 6 m. high).

LAURACEAE

Cryptocarya Wilsonii Guillaumin, sp. nov.

Arbor parva, trunco 30 cm. diam., ramis glabris, foliis ovatis (usque ad 19 cm. \times 10 cm.) breviter acuminatis basi subito cuneatis glabris, nervis lateralibus 5–8-jugis, petiolo 1–1.5 cm. longo. Paniculae usque ad 6 cm. longae axillares, ramulis pedicellisque breviter rufo-velutinis, floribus minimis (1 mm. longis) breviter pedicellatis (sub 1 mm.) vel sessilibus, bracteis minimis lanceolatis in utraque pagina rufo-velutinis, perianthio campanulato fere usque ad medium 6-lobato, segmentis ovatis carinatis extra dense intus sparsius rufo-velutinis, staminibus generis, subsessilibus, connectivis pilosis, antheris lanceolatis apice muticis, staminodiis omnino sessilibus staminibus similibus sed latioribus apiceque acutis, ovario glabro, stylo subulato staminum apicem subattingente; fructus transverse ellipsoidei (2 cm. \times 2.6 cm. \times 2 cm.), pericarpio tenui.

A n e i t y u m : Anelgauhat Bay, scarce in rain-forest at 175–500 m., no. 951 (coll. *J. P. Wilson*) Sept. 1929 (low tree to 30 cm. in diam., leaves large; flowers small, yellow; fruit round 2.5 cm. in diam., seeds eaten by natives).—Vernacular name “Inceohp.”

The fruit resembles particularly that of *C.*¹ *obcordicarpa* Lecard ex Guillaumin of New Caledonia.

Cryptocarya sp.

A n e i t y u m : Anelgauhat Bay, scarce in rain-forest at 300 m., no. 950 (coll. *J. P. Wilson*) Sept. 1929 (small tree; leaves small, pointed, with yellow midrib; flowers white; fruit round, 1.8 cm. diam.)—Vernacular name “Ingeyho.”

Beilschmiedia sp.

A n e i t y u m : west coast, common in rain-forest up to 450 m., no. 964 (coll. *J. P. Wilson*) Sept. 1929 (tall tree up to 60 cm. in diam., leaves medium; flowers small, white; fruit red, 2 cm. long, 1.7 cm. in diam.)—Vernacular name “Nipicgow.”

Endiandra aneityensis Guillaumin, sp. nov.

Arbor parva, 10 m. alta, trunco 22 cm. diam., ramis compressis cortice rubro, novellis rufo-puberulis cito glabris, foliis ovatis (8–12 cm. \times 3–5 cm.) lutescente viridibus apice basique cuneatis pergamentaceis vel leviter coriaceis costae basi excepta glabris penninerviis, in utraque pagina dense reticulato-nervosis, petiolo 1 cm. longo puberulo. Paniculae axillares, circa 5 cm. longae, sparse puberulae, floribus coeruleis distincte (1–3 mm.) pedicellatis, peri-

¹ Owing to a typographical error *C. lifuensis* and *C. macrocarpa* (Bull. Soc. Bot. France, LXXI. 1103. 1925) have been attached to the genus *Cassytha*, but by referring to p. 1105 one finds these species in the key of *Cryptocarya*.

anthio sphaerico 2 mm. diam. extra sparsissime puberulo intus glabro, apice lobis 6 ovato-triangularibus 0.5 mm. longis reflexis glaberrimis, staminibus 3 perianthii ore erectis fere 1 mm. longis glabris, filamentis basi utrinque glandula parva globosa donatis, antheris ovatis, staminodiis 3 glandulis simillimis, ovario glabro ovato in stylum attenuato, stigmatē 2-lobō. Fructus nigri, ellipsoidei (3.5 cm. \times 2.5 cm.).

Anēityum: Anelgauhat Bay, common in rain-forest at 25 m., no. 704 (typus), Feb. 4, 1929 (large tree up to 20 m. high, leaves light green); common in rain-forest at 175–500 m., no. 955 (coll. *J. P. Wilson*), Sept. 1929 (low tree up to 21.5 cm. diam., flowers small, blue; fruit 3 cm. long, 2.5 cm. in diam., edible, eaten by natives).—Vernacular name “Incitray” (under no. 955).

This species is very remarkable on account of the spherical rather than campanulate shape of the tube of the perigone.

Litsea aneityensis Guillaumin, sp. nov.

Arbor magna, 13 m. alta, trunco 25 cm. diam., innovationibus fulvo-tomentosis cito glabris, foliis ovatis (5.5–10 cm. \times 3–6 cm.) leviter coriaceis apice acutis vel subacuminatis basi cuneatis penninerviis, nervis circa 6-jugis, venis subtus dense reticulatis, petiolo 1–1.5 cm. longo. Umbellulae fasciculatae, 1.2 cm. longae, axillares, albae, 4–5-florae, pedunculo 5–8 mm. longo, involucri phyllis 4–5 mm. longis ovatis margine parce ciliatis, pedicello usque ad 5 mm. longo, perigonii tubi lobis 0, staminodiis circa 6, antheris ad laminam lineari-lanceolatam reductis, omnibus filamentis 2-glandulosis dorso sparse ciliatis, ovario glabro. Fructus rubri, ovoidei (2 cm. \times 1.5 cm.) in tubo staminodifero calycem simulante 7 mm. diam. insidentes.

Anēityum: Anelgauhat Bay, common in rain-forest at 70 m., no. 748 (typus), Feb. 12, 1929 (large tree up to 12 m. high; stamens and anthers white); southwest, common in rain-forest at 60 to 275 m., no. 960 (coll. *J. P. Wilson*), Sept. 1929 (low tree up to 40 cm. diam.; flowers small, white; fruit red, 2 cm. long, 1.8 cm. in diam.)—Vernacular name “Incipet” (under no. 960).

This species resembles most *L. minor* Teschn. of New Guinea.

Litsea tannaensis Guillaumin, sp. nov.

Arbor circa 7 m. alta, innovationibus fulvo-tomentosis citissime glabris, foliis ovatis (4.5–7.5 cm. \times 2.5–4 cm.) apice obtusis vel obtuse acuminatis basi late cuneatis leviter coriaceis penninerviis, nervis 5–6-jugis, venis immersis fere inconspicuis, petiolo 0.5–1 cm. longo. Umbellulae singulae vel fasciculatae, ad axillas foliorum vel foliorum delapsorum, 1 cm. longae, albae, 5-florae, pedunculo

5 mm. longo, involucri phyllis 4, 3 mm. longis ovatis margine parce ciliatis, pedicello brevi vel 0, perianthii tubi lobis 0, staminibus 6-9, 3-6 longioribus filamentis antheris 3-plo longioribus glandulis 2 globosis pedicellatis ad apicem munitis, 3-0 interioribus brevioribus filamentis antheris 2-plo longioribus, nonnunquam glandulis pedicellatis ad apicem destitutis, pistillo 0.

Tanna: Lenakel, common in rain-forest at 200 m., no. 109, March 6, 1928 (tree about 7 m. high; flowers white).

This species seems nearest to *L. maluensis* Teschn. of New Guinea from which it is chiefly distinguished by the perianth having no lobes.

HERNANDIACEAE

Hernandia cordigera Viellard in Ann. Sci. Nat. sér. 4, xvi. 62 (1861).

Aneityum: Anelgauhat Bay, common in rain-forest at 50 m., no. 703, Feb. 4, 1929 (large tree up to 20 m. high; petals white; used by the natives for canoe-making). *Tanna*: Lenakel, common in rain-forest at 150 m., no. 125, March 7, 1928 (tree 20 m. high, 70 cm. in diam.). *Erromanga*: Dillon Bay, centre of island, common in rain-forest at 400 m., no. 341, June 1, 1928 (large tree up to 20 m. high; petals dirty cream-colored; fruit 4.5-5.5 cm. long tapering to a blunt point; wood white, soft and used for canoe building).—Also in New Caledonia.

Hernandia peltata Meisner in De Candolle, Prodr. xv. pt. i. 263 (1864).

Aneityum: Utgi, common along seashore at 90 m., no. 1001 (coll. *J. P. Wilson*), Sept. 1929 (large tree to 1 m. diam.; flowers yellow, clustered; fruit round, red, clustered). *Erromanga*: Dillon Bay, common in rain forest and along seashore, sea level, no. 307, May 25, 1928 (large straight tree up to 25 m. high, 75 cm. diam.; petals white, stamens yellow, stigma pale purple; this tree has a very soft wood and is used for canoe-building). *Banks Group*: Vanua Lava, common in rain-forest at sea level, no. 435, July 10, 1928 (large tree, wood used by natives for canoes).—Already found on Efate; also New Caledonia, Fiji, Tonga, Wallis, Cook, Society, Marquesas, Union, Ellice, Marshall, Mariana, Santa Cruz, Solomon, Bismarck and Admiralty Islands, New Guinea and Malaysia.—Vernacular names "Nogogu" (under no. 1001) and "Nehele" (under no. 307).

PROTEACEAE

Kermadecia lutea Guillaumin, sp. nov.

Arbor magna, 20 m. alta, ramis validis primum dense fulvo-pilosis deinde glabris, foliis ovato-lanceolatis (usque ad 14 cm. \times 6 cm.)

primum dense fulvo-pilosis deinde glabris apice acute attenuatis basi cuneatis supra lutescentibus coriaceis, costa supra lutea, nervis 4-jugis subtus prominentibus, venis reticulatis subtus prominentibus, petiolo usque ad 4.5 cm. longo. Inflorescentiae axillares, foliis subaequilongae primum dense fulvo-pilosa, deinde glabrae, racemosae, floribus luteis in ramo circa 3 mm. longo 2-nis oblique sessilibus, bracteis 0, perigonii tubo recto basi oblique dilatato extra fulvo-piloso 1 cm. longo per anthesin uno latere fisso, segmentis concavis lanceolatis dein solutis, antheris ovatis sessilibus, disco unilaterali carnoso, ovario oblique sessili glabro ut stylo cylindrico, stigmate leviter incrassato. Fructus racemosi, in pedicello robusto 1 cm. longo singuli, curvatim ovati, leviter compressi (3-4 cm. \times 2-3 cm. \times 1.5-2 cm.), apice apiculati, nigri, exocarpio tenuissimo, endocarpio 2 mm. crasso osseo, semine 1 valde compresso.

A n e i t y u m : Anelgauhat Bay, common in rain-forest 275 m., no. 901 March 11, 1929 (large tree up to 18 m. high; leaves with light yellow midribs; fruit 4 cm. long, 2.75 cm. in diam.; wood beautifully grained similar to the Queensland silky oak); no. 828, Feb. 28, 1929 (tall tree up to 12 m. high; fruit 3 cm. long, 2.5 cm. in diam., yellow when ripe).—*T a n n a* : Mt. Tokosh Meru, rain-forest, 400 m., no. 167 (typus) March 15, 1928 (flowers yellow; fruit black).—Vernacular name "Silky Oak" (under no. 167).

This species resembles, particularly in its leaves, *Adenostephanus austro-caledonicus* Brongn. & Gris of New Caledonia, which, as also Benthham and Hooker believe, must be a *Kermadecia*, but its flowers are unknown.

Grevillea elaeocarpifolia Guillaumin, sp. nov.

Arbor magna, 12 m. alta, ramis crassis cinereis primum rubiginose tomentosis deinde glabris, foliis lanceolatis (usque ad 14 cm. \times 3.5 cm.) apice acutis mucronulatisque basi acutis, nervis 15-18-jugis tenuibus infra prominulis, venis reticulatis immersis, petiolo circa 1 cm. longo primum rubiginose tomentoso mox glabro. Inflorescentiae e ramis veteribus ortae, racemosae, usque ad 15 cm. longae, sparse tomentosae, floribus luteis pedicello 1 cm. longo suffultis, perigonii tubo basi oblique dilatato extra sparse puberulo 1.5 cm. longo per anthesin uno latere fisso, segmentis ovatis concavis tarde solutis, antheris sessilibus ovatis, disco unilaterali carnoso, ovario stipitato stipite 3 mm. longo, stylo 13-14 mm. longo apice incrassato, stigmate terminali conico. Fructus indehiscentes, maturitate lutei, curvatim ovoidei, lateraliter compressi (2.5 cm. \times 2.3 cm. \times 1.8 cm.), apice apiculati, pericarpio usque ad 5 mm. crasso lignoso, seminibus 2 plano-compressis orbicularibus margine alatis.

Tanna: Lenakel, not common in rain-forest at 200 m., no. 95 (typus) March 5, 1928 (tree about 12 m. high; flowers yellow; fruit yellow when ripe; nuts eaten by natives). *Eromanga*: Dillon Bay, not common in rain-forest at 400 m., no. 350, June 1, 1928 (tree up to 10 m. high; fruit yellow when ripe; nuts eaten by natives).—Vernacular names “Ngye-ngye” (under no. 95) and “Ugkom-ukom” (under no. 350).

The genus is essentially Australian and New Caledonian (with the exception of the Loyalty Islands), but has two representatives in New Guinea.

THYMELACEACEAE

Wikstroemia viridiflora Meisner in Denkschr. Bot. Ges. Regensb. III. 286 (1841).

Tanna: Lenakel, common in rain-forest at 200 m., no. 107, March 6, 1928 (small shrub 2 m. high; flowers cream-colored). *Eromanga*: Dillon Bay, common in poor red soil, bracken country at 300 m., no. 302, May 24, 1928 (small shrub 2–3 m. high; flowers cream-colored; bark thrown into pools to stupefy fish so they can be caught by hand).—Also New Caledonia, Loyalty, Fiji and Cook Islands and Australia (Queensland, New South Wales, North Australia).—Vernacular name “Tao-wap” (under no. 302).

LORANTHACEAE

Elytranthe banksiana Guillaumin, sp. nov.

Glaberrima, ramis gracilibus, foliis spathulatis (5–8 cm. \times 2–2.5 cm.) apice rotundatis basin versus in petiolum indistinctum attenuatis crassis, nervis immersis. Inflorescentiae racemosae (?), pedicello 5 mm. longo, bractea late ovata 1 mm. longa, calycis parte libera tubum 1 mm. longum leviter patulum formante, petalis aureis apice rubris, tubo 4 cm. longo, supra medium sensim dilatato, longitudinaliter costato, lobis 5–6 linearibus reflexis 1.5 cm. longis, staminibus 5–6 erectis corollae lobis brevioribus, antheris filamentis leviter brevioribus linearibus, ovario omnino infero, stylo filiformi basi conice incrassato stamina superante, stigmata capitato.

Banks Group: Vanua Lava, common in rain-forest at 300 m. no. 453, July 10, 1928 (parasitic plant growing on a tree where sunlight is available; very pretty golden petals with red ends).

Loranthus aneityensis Guillaumin, sp. nov.

Ramis gracilibus cinereis, foliis obovatis (3–4 cm. \times 2–2.5 cm.) apice rotundatis basi plus minusve subito in petiolum indistinctum cuneatis valde coriaceis, venis inconspicuis. Inflorescentiae 3 cm. longae, umbellatim cymosae, ramis rubiginoso-puberulis, bractea

triangulări acuta vel ovata extra dense rubiginos-opuberula, calycis parte libera tubum brevissimum campanulatum formante, petalis aurantiacis liberis 5 lineari-lanceolatis 2 cm. longis extra sparse puberulis, staminibus 5 erectis corollae lobis aequilongis, antheris filamentis aequilongis apice muticis, ovario omnino infero, obconico, dense rubiginoso-puberulo, stylo filiformi petalis aequilongo, basi disco annulari cincto, stigmatē capitellato. Fructus ovoidei (5 mm. \times 4 mm.), minimi, rubiginose puberuli.

Aneityum: Anelgauhat Bay, common in rain-forest at 300 m., no. 753, Feb. 12, 1929 (parasite growing upon trees in the open partly cleared scrub land; flowers orange-colored).

Loranthus ficivorus Guillaumin, sp. nov.

Ramis sat robustis dense rugose lenticellatis cinereo-fulvis, foliis late obovatis (5–7 cm. \times 3.5–5 cm.) apice rotundatis basi in petiolum indistinctum cuneatis valde coriaceis, venis 2-jugis immersis. Inflorescentiae 4 cm. longae, umbellatim cymosae, ramis fulvo-puberulis, bractea ovata extra fulvo-puberula, calycis parte libera tubum brevissimum extra fulvo-puberulum formante, petalis basi roseis apice luteis liberis 5 linearibus ad 2.5 cm. longis, staminibus corollae lobis leviter brevioribus, antheris filamentis 1.5-plo brevioribus, connectivo apice leviter globose producto, ovario omnino infero turbinate fulvo-puberulo, stylo filiformi petalis aequilongo, basi disco annulari cincto, stigmatē capitellato.

Tanna: Lenakel, common in rain-forest at 60 m. no. 94, March 5, 1928 (parasitic on *Ficus*; flowers pink at base with yellow tips).

The specimen no. 87, March 3, 1928, from *Tanna*: Lenakel, common in rain-forest at 150 m. (commonly parasitic on rain-forest trees) with less thick leaves and ellipsoid fruit (1 cm. \times 0.6 cm.) probably belongs to the same species.

SANTALACEAE

Santalum austro-caledonicum Vieillard in Ann. Sci. Nat. sér. 4, xvi. 61 (1861).

Aneityum: Anelgauhat Bay, common in rain-forests at 180 m., no. 814, Feb. 23, 1929 (small tree up to 9 m. high; flowers cream-colored; fruit purple when ripe; this is exported as the sandalwood of commerce). *Eromanga*: Dillon Bay, common in rain-forest at 300 m., no. 287, May 23, 1928 (tree up to 20 m. high; leaves light green above, silvery underneath; flowers cream-colored; fruit 1.5 cm. long, 1 cm. in diam., black when ripe; the sandalwood of commerce).—Already recorded from *Aneityum* and *Eromanga*; also New Caledonia and Loyalty Islands.—Vernacular name "Worlu" (under no. 287).

EUPHORBIACEAE

Euphorbia obliqua Endlicher, Prodr. Fl. Norf. 85 (1833).

Eromanga: Dillon Bay, common on rocky beach at sea level, no. 257, May 15, 1928 (small plant about 25 cm. high, growing in the crevices of rocks; flowers white; sap used in conjunction with charcoal for tattooing, producing blue marks).—Already found on Aneityum and on Eromanga; also New Caledonia, Loyalty, Norfolk and Tonga Islands.—Vernacular name "Uripatepu."

Phyllanthus, sp. nov. ?

Aneityum: Anelgauhat Bay, common in rain-forest up to 150 m., no. 912, March 11, 1929 (small tree up to 6 m. high; flowers brown).

Phyllanthus sp.

Aneityum: Anelgauhat Bay, common in rain-forest at sea level, no. 908, March 11, 1929 (small tree up to 6 m. high; fruit 0.5 cm. long, light pink when ripe). *Tanna*: Lenakel, common in rain-forest at 100 m., no. 73, March 1, 1928 (small tree about 8 m. high). *Eromanga*: Dillon Bay, common in rain-forest at 300 m., no. 274, May 17, 1928 (small tree up to 10 m. high; fruit red; leaves crushed and used by natives for fevers).

This seems to belong to the same group as *P. Gaudichaudii* Muell. Arg. of the Samoa and Tonga Islands, New Guinea, Aru Island and the Mariana Islands.—Vernacular name "Narmlee" (under no. 274).

Glochidion tannaense Guillaumin, sp. nov.

Arbor, ramulis leviter compressis glabris, foliis lanceolatis (usque ad 7 cm. \times 3 cm.) apice basique acutis rigide membranaceis infra pallidioribus, nervis circa 7-jugis tenuissimis, petiolo 4–5 mm. longo, stipulis lineari-lanceolatis cito caducis petiolo 2-plo brevioribus, floribus ♀ circa 6, pedicellis circa 5 mm. longis gracilibus apicem versus leviter incrassatis, tepalis 6 vix 1 mm. longis ovatis obtusis, ovario glabro 10-loculari, columna stylari conica superne angustata et ovario continua.

Tanna: Lenakel, common in rain-forest at 200 m., no. 91, March 5, 1928 (tree of large dimensions with numerous roots of the banyan type; flowers yellow).

Though the staminate flowers are not known, there can be no doubt, that it is a *Glochidion* which should be placed near *G. lucidum* Bl. of Malaysia and *G. novo-guineense* K. Schum. of New Guinea. Could this be the *Glochidion* sp. found on Tanna by Forster?

Hemicyclea Deplanchei (Brongn. & Gris) Baillon apud Guillaumin in Ann. Mus. Col. Marseille, sér. 2, ix. 224 (1911).

Aneityum: Anelgauhah Bay, common in rain-forest at 150 m., no. 933, March 17, 1929 (large tree up to 18 m. high; fruit 1.4 cm. long, 1 cm. in diam., yellow when ripe).—Also New Caledonia.

Bischofia javanica Blume, Bijdr. 1168 (1826).

Eromanga: Dillon Bay, common in rain-forest at sea level, no. 310, May 26, 1928 (large tree up to 25 m. high; bark is boiled in salt water and applied to cuts).—Also New Caledonia, Australia (Queensland), Fiji, Tonga, Cook and Society Islands and Malaysia.—Vernacular name "No-ghor."

Aleurites moluccana Willdenow, Sp. Pl. iv. 590 (1805).

Eromanga: Dillon Bay, common in rain-forest at sea level, no. 242, May 14, 1928 (very fine tree with a straight barrel up to 20 m. high; kernel of fruit threaded on a cocoanut fibre used as a candle).—Already found on Efate; also New Caledonia, Loyalty Islands, Australia (Queensland), New Zealand, Fiji, Tonga, Samoa, Cook, Society, Marquesas, Gambier and Mariana Islands, New Guinea, Malaysia and Hawaii.—Vernacular name "Candle-nut."

Croton insularis Baillon in Adansonia, II. 217 (1861-62).

Aneityum: Aname, locally common in lower ranges up to 150 m., no. 988 (coll. *J. P. Wilson*), Sept. 1929 (small tree to 23 cm. in diam.; leaves broad; flowers small, brown; fruit small 0.6 cm. in diam.). *Eromanga*: Dillon Bay, common in rain-forest at sea-level, no. 267, May 17, 1928 (small tree up to 15 m. high; leaves green above, silvery brown underneath).—Also New Caledonia, Loyalty Islands, Australia (Queensland, New South Wales).—Vernacular names "Nalipes" (under no. 267), "Imrath" (under no. 988).

Codiaeum variegatum (L.) Bl. var. *moluccanum* (Decne.) Mueller Arg. in DeCandolle, Prodr. xv. pt. II. 1119 (1866).

Banks Group: Vanua Lava, common in rain-forest at sea level, no. 409, June 5, 1928 (small tree up to 12 m., high; flowers white); no. 423, July 6, 1928 (small tree up to 7 m. high; leaves dark green).

Codiaeum variegatum (L.) Bl. var. *pictum* (Lodd.) Mueller Arg. in DeCandolle, Prodr. xv. pt. II. 1119 (1866).

Tanna: Lenakel, common in rain-forest at 100 m. no. 31, Feb. 21, 1928 (shrub up to 6 m. high, with pretty variegated leaves).

This species has been found already on Aneityum, Tanna, Efate, and Mallicolo; also New Caledonia, Loyalty Islands, Australia (Queensland), Fiji, Tonga, Samoa, Cook, Marshall, Caroline, Mariana, Santa Cruz, Solomon, Bismarck and Admiralty Islands, New Guinea and Malaysia.

Alphandia furfuracea Baillon in *Adansonia*, xi. 86 (1873).

Aneityum: Anelgauhat Bay, common in rain-forest at 90 m. no. 809, Feb. 23, 1929 (large tree up to 12 m. high; leaves dark green, midrib yellow; flowers creamy yellow; fruit 2.5 cm. long, 2 cm. in diam., light yellow).—Also New Caledonia.

Fontainea Pancheri (Baill.) Heckel, Thèse Inaug. Montpell. 1870, apud Baillon in *Adansonia* xi. 80 (1873).

Aneityum: Anelgauhat Bay, common in rain-forest at sea level, no. 906, March 11, 1929 (small tree up to 9 m. high; fruit 5 cm. long, 4 cm. in diam., orange-colored when ripe; this tree contains a remarkable poison throughout and is used for poisoning fish.)—Also New Caledonia and Loyalty Island.

Claoxylon insulanum Mueller Arg. in *Linnaea* xxxiv. 164 (1865-66).

Aneityum: south west, common in rain-forest at 60-300 m. no. 958A (coll. *J. P. Wilson*), Sept. 1929 (small tree, trunk 22.5 cm. in diam.; flowers small, white; fruit a small berry). *Efate*: Undine Bay, common in rain-forest at 500 m., no. 232, April 28, 1928 (tree 10-15 m. high).—Also New Caledonia and Loyalty Islands.—Vernacular name "Namchrai" (under no. 958A).

Claoxylon taitense Muell. Arg. var. *neo-ebudicum* Guillaumin, var. nov.

A planta taitensi differt racemis brevioribus (2.5-6 cm. longis), floribus 3-5-fasciculatis, glabris, petioli glandulis subulatis glandulis minimis adjunctis.

Eromanga: Dillon Bay, common in rain-forest at 400 m., no. 347, June 1, 1928 (tree about 15 m. high; flowers white).—Vernacular name "Ney-emptey."

The type of the species occurs in Tahiti and New Caledonia.

Acalypha grandis Bentham in *Lond. Jour. Bot.* ii. 232 (1843).

Tanna: Lenakel, common in heavy rain-forest soil at sea level, no. 16, Feb. 21, 1928 (small tree growing in semi-cleared land).—Already found on *Aneityum*; also New Caledonia, Loyalty, Fiji, Wallis, Tonga, Samoa, Bismarck and Admiralty Islands, New Guinea, Moluccas and Malaysia.

Acalypha neo-caledonica Mueller Arg. in *DeCandolle, Prodr.* xv. pt. ii. 812 (1866).

Tanna: Lenakel, common in rain-forest soil at sea level, no. 21, Feb. 21, 1928 (small shrub up to 4 m. high). *Eromanga*: Dillon Bay, common in rain forest at 300 m., no. 383, June 8, 1928 shrub up to 5 m. high).—Already found on *Aneityum*; also New

Caledonia and Loyalty Islands.—Vernacular name “Nau-nompe pura-puri” (under no. 383).

Acalypha sp., an *A. Forsteriana* Muell. Arg.?

Eromanga: Dillon Bay, common in rain-forest at sea level, no. 248, May 15, 1928 (small tree up to 5 m. high).—Vernacular name “Nau-numpey.”

Identical with no. 1 of Levat from Efate, vernacular name “Noc-fis.”

Acalypha Forsteriana, endemic in the New Hebrides, has been already found on Tanna and Efate.

Cleidion angustifolium Pax & K. Hoffmann in Engler, Pflanzenr. iv.-147. pt. vii. 293 (Euphorbiac.) (1914).

Aneityum: south west, common in lower hills up to 60 m. no. 959 (coll. *J. P. Wilson*), Sept. 1929 (small tree up to 25 cm. diam.; flowers very small, white; fruit a small berry).—Also New Caledonia.—Vernacular name “Nijivit.”

The character “ovarium sparsissime adpresse pilosum” brings the species not near *C. spathulatum* Baill. but near *C. Vieillardii* Baill. var. *acutifolium* Muell. Arg.

Cleidion Vieillardii Baill. var. *acutifolium* Mueller Arg. in De Candolle, Prodr. xv. pt. ii. 986 (1866).

Aneityum: Anelgauhat Bay, common in rain-forest at 240 m., no. 909, March 11, 1929 (small tree up to 9 m. high, flowers minute, white).—Also New Caledonia.

Macaranga Tanarius (L.) Mueller Arg. in DeCandolle, Prodr. xv. pt. ii. 997 (1866).

Tanna: Lenakel, common in heavy rain-forest soil at sea level, no. 17, Feb. 21, 1928 (tree up to 15 m. high).—Already found on Tanna; also New Caledonia, Australia (Queensland, North Australia, New South Wales), Bismarck Islands, New Guinea, Moluccas and Malaysia.

The plant from Tanna corresponds to var. *genuina* Muell. Arg., while the plant of New Caledonia is pubescent, but as indicated by J. J. Smith and later by Pax and Hoffmann, all intermediate stages are found.

It is very probable that *Ricinus Mappa* Forst. also collected on Tanna (Forster, no. 213) belongs to this species.

Macaranga sp.

Tanna: Lenakel, common in rain-forest soil at 100 m., no. 37, Feb. 21, 1928 (tree 12–15 m. high, about 20–40 cm. diam.). *Eromanga*: Dillon Bay, common in rain-forest at 300 m., no. 319,

May 28, 1928 (tree about 10 m. high; dried leaf bandaged over sore to heal it).—Vernacular name "Norvo-among" (under no. 319).

Macaranga sp.

Aneityum: Anelgauhat Bay, common in rain-forest at sea level, no. 708, Feb. 10, 1929 (small tree up to 10 m. high; leaves dark green above, silvery underneath; stamens and anthers cream-colored). **Banks Group**: Vanua Lava, common in rain-forest at sea level, no. 440, July 9, 1928 (small tree up to 7 m. high).

These four specimens all staminate possibly belong to the same species.

Homalanthus ebracteatus Guillaumin, sp. nov.

Arbor 8 m. alta, trunco 15 cm. diam. omnino glabra, ramis tortuosis, foliis rhomboideo-ovatis (2–3.5 cm. \times 2–4 cm.) apice rotundatis vel brevissime acutis basi obtuse truncatis, petiolo 1–3 cm. longo apice 2-glanduloso. Racemi erecti, circa 4 cm. longi, floribus singulis ♂ ebracteatis, ♀ bractea naviculari apice cuspidata basi cordata breviter pedicellata involucriatis, floribus ♂ patentibus, pedicello 2 cm. longo supra medium vel ad apicem glandulis 2 hemisphaericis notato, sepalo parvo reniformi, antheris circa 20, floribus ♀ ad racemi basin 1–2 nutantibus, pedicello 3 mm. longo, tepalis 3 semi-circularibus bene distinctis, stylo brevi, stigmatibus 3-plo longioribus apice 2-lobis. Fructus ovoideo-compressi, carpellorum dorso carinatis.

Tanna: Lenakel, common in rich rain-forest soil at 200 m. no. 47, Feb. 24, 1928 (tree about 8 m. high, about 15 cm. diam.).

The pedicels of the staminate flowers without bracts at the base but furnished with two glands below the middle represent an entirely new type in the genus which is worthy to constitute a new series **EBRACTEATI**.

Homalanthus longipes Pax & K. Hoffmann in Engler, Pflanzenr. iv.-147. pt. v. 51 (Euphorbiac.) (1912). **Eromanga**: Dillon Bay, common in rain-forest at sea level, no. 263, May 17, 1928 (tree up to 15 m. high; leaves silvery underneath).—Already found on Eromanga.—Vernacular name "Nemtar-bwar."

The specimen lacks pistillate flowers.

Homalanthus nutans (Forst.) Pax var.

Aneityum: Anelgauhat Bay, common in rain-forest at 600 m., no. 976 (coll. J. P. Wilson), Aug. 1929 (tree to 0.30 m. diam.; flowers very small, yellow; fruit flattened 1 cm. long, 0.7 cm. in diam.).—Already found on Tanna, Eromanga and Efate; also New Caledonia, Loyalty, Fiji, Tonga, Samoa, and Society Islands.—Vernacular name "Ettaing."

Excoecaria Agallocha Linnaeus, Syst. Nat. ed. 10, 1288 (1759).

Aneityum: Anelgauhat Bay, common along seashore, no. 694, Feb. 4, 1929 (tree up to 15 m. high; sap milky). *Tanna*: Lenakel, common in heavy sandy soil of seashore, no. 1, Feb. 20, 1928 (spreading tree about 12 m. high, with numerous spreading stems or coppice growth; fruit dark brown when ripe; sap milky).—Already found on Efate; also New Caledonia, Loyalty Islands, Australia (Queensland, North Australia), Norfolk Island, Fiji, Tonga, Caroline, Mariana, Solomon and Bismarck Islands, New Guinea and Malaysia.

BALANOPSIDACEAE

Trilocularia pedicellata Guillaumin, sp. nov.

Arbor parva, ultra 6 m. alta, ramis erectis teretibus glabris, foliis alternis ad ramulorum apicem congestis ovatis (4–7 cm. \times 2–4 cm.) valde obtusis basi rotundatis leviter coriaceis, marginibus recurvatis, nervis vix conspicuis concoloribus, petiolo 0.5–1 cm. longo. Fructus 1 cm. pedicellati, bracteis 4 minimis sparsis, bracteis involucrantibus 8, interioribus sensim majoribus et 5 mm. longis, orbicularibus margine ciliatis, glandi simillimi, circa 1.5 cm. \times 1 cm., stylorum 3 usque ad basin 2-fidorum reliquiis coronati, loculis 3.

Banks Group: Vanua Lava, common in rain-forest on tops of high mountains at 600 m., no. 476, July 12, 1928 (small tree up to 6 m. high).

This species on account of its pedicelled fruit is very distinct from *T. sparsiflora* Schlechter of New Caledonia, the only species of the genus hitherto known.

The family thus was represented outside of New Caledonia only by a single species found only once in Queensland.

CELTIDACEAE

Celtis paniculata Planchon in Ann. Sci. Nat. sér. 3, x. 305 (1848).

Aneityum: Anelgauhat Bay, common in rain-forest at sea level, no. 927, March 19, 1929 (large tree up to 15 m. high; fruit black when ripe).—Also New Caledonia, Loyalty Islands, Australia (Queensland, New South Wales, North Australia), Norfolk Island and Society Islands.

Trema Vieillardii Schlechter in Engler, Bot. Jahrb. xxxix. 96 (1906).

Aneityum: Anelgauhat Bay, common in rain-forest at sea level, no. 717, Feb. 9, 1929 (small tree up to 15 m. high; fruit brown-black when ripe). *Eromanga*: Dillon Bay, common in rain-forest at sea level, no. 398, June 8, 1928 (tree up to 10 m. high;

used for rafters of native houses).—Also New Caledonia and Loyalty Islands.—Vernacular name “Nendog” (under no. 398).

MORACEAE

Pseudomorus Brunoniana Bureau in Ann. Sci. Nat. sér. 5, xi. 371 (1869).

Aneityum: Anelgauhat Bay, common on seashore, no. 926, March 17, 1929 (small tree up to 9 m. high).—Also New Caledonia, Australia (Queensland, New South Wales), Norfolk Island, New Guinea and Hawaii.

ARTOCARPACEAE

Ficus L.

Determined by V. S. SUMMERHAYES

Sect. PALAEOMORPHE

Ficus Decaisneana Miquel, Fl. Ind. Bat. i. pt. ii. 312 (1859).

Ficus philippinensis var. *sessilis* Bureau in Ann. Sci. Nat. sér. 5, xiv. 253 (1872).

Banks Group: Vanua Lava; sea level, rain-forest, common, no. 493, July 18, 1928 (large tree 20 m. high). **Eromanga**: Dillon Bay, sea level, rain-forest, common, no. 265, May 17, 1928 (Fig with straight barrel instead of the usual contorted type; fruit yellow to purple when ripe); alt. 300 m., rain-forest, common, no. 395, June 8, 1928 (small tree 10 m. high).—Vernacular names “Nevelisi” (under no. 395) and “Nervelisen” (under no. 265).

Careful comparison of these specimens with some of those cited by Bureau from New Caledonia and with others from New Guinea and eastern Malaya has convinced me that they all belong to the same species. Although Bureau compares his new variety with *F. subulata* Bl., his description does not mention any hermaphrodite flowers, only male and female ones, and does not specify whether the latter are perfect or galled. The New Caledonian specimens at Kew examined by me bear female receptacles only, but both types occur on the New Hebridean specimens and in the galled receptacles good hermaphrodite flowers were found. In King's monograph the perianth of *F. Decaisneana* is shown as glabrous but this does not seem to be so in any of the specimens I have seen, the lobes being always slightly pubescent or ciliolate and sometimes thickly so. They are, however, always quite free, which sharply distinguishes the species from *F. subulata*, the vegetative characters of which are very similar.

The length of the receptacular stalk is not a constant feature

in *F. Decaisneana* and cannot in my opinion be used for separating a variety from the type. There are specimens at Kew with almost sessile receptacles from almost the whole range of the species although they are commonest in New Caledonia and the New Hebrides.

Ficus neo-ebudarum Summerhayes, sp. nov.

Arbor parva usque 10 m. alta vel frutex scandens; ramuli cortice brunneo primo sparse scabridulo leviter sulcato demum fere laevi obtecti. Folia alterna, breviter petiolata, oblique et inaequaliter ovata, apice breviter acuminata, basi late cuneata vel saepius rotundata, 7–14 cm. longa, 3.5–7 cm. lata, coriacea, omnino glabra, laevia, costa supra vix prominula subtus prominente, nervis lateralibus utrinsecus 6–8 e costa angulo 55–70° exeuntibus prope marginem arcuatim conjunctis supra vix prominulis subtus prominentibus, rete venularum distincto saepe siccitate distinctissimo sed vix prominulo; petiolus crassiusculus, 6–15 mm. longus, mox cortice in laminas parvas tenuissimas decorticante obtectus; stipulae lanceolatae, acuminatae, glabrae. Receptacula axillaria, solitaria vel gemina, alia flores ♂ et ♀ cecidiophoros alia flores ♀ includentia, pedunculata, subsphaeroidea, rubra, 10–12 mm. diametro, sparse scabridula, umbicilo prominulo, ostioli bracteis subprominentibus; pedunculus falsus (stipes receptaculi) gracilis, 4–6 mm. longus, basi bracteis tribus ovatis acutis 1 mm. longis instructus, pedunculo vero interdum brevi. Flores ♂ prope ostiolum, sessiles vel saepissime pedicellati, perianthii segmentis 4 linearibus vel anguste lanceolatis acutis, ovarium et antheram superantibus basi sparse pubescentibus; stamen 1, anthera 1 mm. longa; ovarium cecidiophorum ellipsoideum, stylo infra-apicali brevi; pedicellus pubescens. Flores ♀ cecidiophori sessiles vel usque 3 mm. longe pedicellati, perianthii segmentis 3–4 eis florum ♂ similibus; ovarium ellipsoideum, 1.5 mm. longum, laeve, stylo infra-apicali, stigmate parvo clavato. Flores ♀ sessiles vel usque 1.5 mm. longe pedicellati, perianthio gamophyllo demum irregulariter fisso quam ovario longiore inferne pubescente; ovarium reniformi-ellipsoideum, 2 mm. longum, rugulosum, stylo infra-apicali vel laterali, stigmate clavato.

Tanna: Lenakel, alt. 150 m., rain-forest, common, no. 79, March 3, 1928 (small tree 10 m. high). Aneityum: west coast, Aname, alt. 150 m., lower ranges and sea-shore, common, no. 995 (coll. J. P. Wilson) (type), Sept. 1929 (large vine on forest trees; flowers red, small; fruit red, 12 mm. diameter).—Vernacular name “Nedeug” (under no. 995).

A very close relative of *F. tinctoria* Forst. from which it differs

in the smaller, definitely acuminate leaves and the larger flowers, of which the perianth is only sparsely pubescent at the base. There are specimens of *F. tinctoria* at Kew from Tahiti, Tonga, Samoa and Fiji and these are remarkably constant in the features mentioned above.

Sect. UROSTIGMA

Ficus acrorrhyncha Summerhayes, sp. nov.

Arbor magna, trunco 2-3 m. diametro. Ramuli teretes, glabri, demum cortice pallide brunneo leviter ruguloso obtecti, lenticellis \pm rotundatis pallidis instructi. Folia petiolata, elliptica, oblongo-elliptica vel ovato-elliptica, apice subito anguste et retrorsum acuminata, basi obtusa, latissime cuneata vel subrotundata, 5-10 cm. longa, 3-6 cm. lata, utrinque glabra, supra praesertim juniora subnitida, costa supra impressa subtus prominente, nervis lateralibus utrinsecus 7-10 rectis vel levissime curvatis basalibus angulo 50-60° ceteris angulo 60° e costa exeuntibus supra prominulis subtus prominentibus nervo submarginali leviter curvato conjunctis, nervis secundariis parallelis crebris, rete venularum subtus distinctissimo; petiolus gracilis, 1-2.5 cm. longus, supra canaliculatus, glaber; stipulae lanceolatae, acuminatae, extra adpresse sericeo-pubescentes. Receptacula axillaria, solitaria, sessilia, ellipsoidea vel subglobosa, circiter 15 mm. longa, 10-12 mm. diametro, siccitate rugosa, glabra, lenticellis rotundatis, ostioli bracteis paulo prominentibus, basi bracteis tribus late reniformibus arcte adpressis instructa. Flores σ^7 , φ et φ cecidiophori commixti. Flores σ^7 longe pedicellati, perianthii segmentis 4 liberis obovatis vel obovato-orbicularibus 1 mm. longis glabris stamen singulum arcte includentibus. Flores φ cecidiophori pedicellati, perianthii segmentis eis florum σ^7 similibus, ovario sessili ellipsoideo 1.5 mm. longo, stylo 0.5 mm. longo, stigmate breviter clavato. Flores φ breviter pedicellati vel saepius sessiles, perianthii segmentis 3-4 ovatis vel lanceolatis 0.7 mm. longis glabris, ovario ovoideo 1.3 mm. longo, stylo 2 mm. longo, stigmate cylindraceo-clavato 0.7 mm. longo.

A n e i t y u m : Umage, alt. up to 460 m., rain-forest, common, no. 999 (coll. *J. P. Wilson*), Sept. 1929, (large tree up to 3-4 m. diam.; flowers small, yellow; fruit 15 mm. diam.).—Vernacular name "Nepluth."

This typical member of sect. *Urostigma* is allied to *F. dictyophlebia* F. Muell., *F. retusa* L. and *F. benjamina* L., from all of which it is easily distinguished by the very abrupt and narrow acumen to the leaves. *F. retusa* has shorter and stouter petioles while the fruit possesses a distinct calyculus. In *F. benjamina*

and *F. dictyophlebia* the leaves are more gradually acute with the veins much more prominent on the upper surface and the petioles are shorter, while the fruits are smaller in *F. benjamina*. Those of *F. dictyophlebia* are unknown.

Ficus austro-caledonica Bureau in Ann. Sci. Nat. sér. 5, xiv. 267 (1872).

A n e i t y u m: Anelgauhat Bay, alt. 240 m., rain-forest, common, no. 862, March 5, 1929 (small tree 6 m. high; fruit 18 mm. long, 22 mm. diam., purple when ripe); s. w. coast, alt. up to 600 m., rain-forest, common, no. 975 (coll. *J. P. Wilson*), Aug. 1929 (small tree 45 cm. diam.; flowers red; fruit 18 mm. diam., red).—Vernacular name “Natinaia” (under no. 975).

This species strongly resembles *F. granatum* Forst. in leaf characters. It may, however, be distinguished by the slightly different venation of the leaves, the smaller receptacles with an easily detachable skin, the inside of the receptacles and the stalks of the flowers being almost or quite glabrous, and by the perianth of the female and gall flowers splitting irregularly into usually broad portions. In *F. granatum* the female perianth consists of five free, linear, acute segments which usually considerably overtop the ovary or achene.

Ficus glandifera Summerhayes, sp. nov.

Arbor magna, habitu *F. indicæ* L. similis. Ramuli crassi, juniores sparsiuscule pubescentes, demum glabrescentes, cortice brunneo obtecti, cicatricibus foliorum et stipularum delapsorum valde notati. Folia petiolata, late ovata, apice breviter acuminata, acuta, basi obtusissima vel saepius rotundata, 7–14 cm. longa, 4–8 cm. lata, costa supra impressa subtus prominente, nervis lateralibus utrinsecus 20–30 parallelis e costa angulo 70–80° exeuntibus utrinque distinctis supra prominulis nervo submarginali curvato conjunctis, nervis secundariis numerosis subparallelis crebris, rete venularum subtus distincto, coriacea, supra subnitentia, utrinque glabra; petiolus pro rata gracilis, supra leviter canaliculatus, 3–4.5 cm. longus, glaber; stipulae non visae, ut videtur caducae. Receptacula axillaria, singula vel gemina, sessilia vel subsessilia, oblongo-ellipsoidea, circiter 4.5 cm. longa, 2.5 cm. diametro, apice in mammillam 5 mm. diametro producta, ostiolo ipso leviter depresso bracteis haud manifestis, bracteis basalibus in cupulam circiter 1 cm. longam breviter pubescentem receptaculo adnatam connatis, receptacula ergo glandes Querci specierum simulantia; pedunculus usque 4 mm. longus, saepius brevissimus, 4 mm. diametro. Flores ♂, ♀ et ♀ cecidiophori commixti.

Flores ♂ longipedicellati, perianthii segmentis 4 liberis ellipticis vel ovatis valde concavis vix 1 mm. longis glabris stamen singulum arcte includentibus, pedicello bracteis duabus lanceolatis instructo. Flores ♀ cecidiophori pedicellati vel rarius sessiles, perianthii segmentis eis florum ♂ similibus, ovario sessili, stylo brevi, stigmate clavato. Flores ♀ sessiles, ovario ovoideo 1.5 mm. longo, stylo infra-apicali 2.5 mm. longo, stigmate minuto.

Tanna : Lenakel, alt. 200 m., rain-forest, common, no. 80, March 3, 1928 (large tree of grand proportions with many roots, "4 m. in diam."; fruit orange-colored). Aneityum : Anelgauhat Bay, sea level, rain-forest, common, no. 802, (type), Feb. 21, 1929 (large tree of spreading banyan type, very beautiful; fruit orange-color when ripe, 4.5 cm. long, 2.5 cm. in diam.).

The species, with its remarkable acorn-like fruit, is allied to a group of four species occurring in Queensland, viz: *F. cylindrica* Warb., *F. Baileyana* Domin, *F. crassipes* F. M. Bailey and *F. Watkinsiana* F. M. Bailey. The two last-named differ in having the tip of the fruit drawn out into a point, as well as in the shape of the leaves and other features. *F. cylindrica* is the most closely related to *F. glandifera*, but differs in the possession of larger, relatively narrower oblong leaves with different venation and longer petioles, in the receptacles being definitely stalked and the cupule at the base being relatively smaller. *F. Baileyana* has leaves very similar to those of our species but the receptacles are much smaller, and have a poorly developed bracteal disc at the base and a slender stalk.

Ficus granatum Forster, Pl. Esc. 37 (1786).

Erromanga : Dillon Bay, alt. 400 m., rain-forest, common, no. 324, May 29, 1928 (large tree 25 m. high; leaves bright green; inside bark used to make cloth as it is glutinous). Tanna : Lenakel, alt. 100 m., rain-forest, common, no. 124, March 7, 1928 (tree 20 m. high; fruit 3-4 at end of each branch, pink when ripe, 4 cm. long, 3 cm. diam.). Aneityum : Anelgauhat Bay, alt. 30 m., rain-forest, common, no. 732, Feb. 11, 1929 (large tree 18 m. high; fruit red when ripe); alt. 15 to 450 m., common, no. 956 (coll. J. P. Wilson), Sept. 1929 (low tree 60 cm. diam.; leaves heavily veined; flowers small, red; fruit brown, edible).—Vernacular names "Nating" (under no. 956) and "Nah-tong" (under no. 324).

A striking species of sect. *Urostigma* which is closely allied to *F. callosa* Willd. and *F. austro-caledonica* Bureau. The differences between it and the latter are mentioned under that species. From *F. callosa*, *F. granatum* is distinguished by its gradually pointed

leaves with the main lateral nerves joining near the margin more simply, the receptacles being red or purple when ripe, and being thickly hairy inside, this also applying to the pedicels of the flowers. In general floral and vegetative characters the species are otherwise very similar.

Ficus obliqua Forster, Prodr. Fl. Ins. Austral. 77 (1786).

E r o m a n g a : Dillon Bay, sea level, rain-forest, no. 253, May 15, 1928 (common throughout group growing into large tree of many branches and roots; fruit orange-color). *T a n n a* : Lenakel, alt. 200 m., rain-forest soil, common, no. 67, Feb. 24, 1928 (large tree 15–20 m. high, 60 cm. to 1 m. in diameter; fruit brown when ripe). *A n e i t y u m* : Anelgauhat Bay, sea shore, rain-forest, common, no. 781, Feb. 19, 1929 (large tree with spreading head; fruit orange-color when ripe).—Vernacular name “Nar-evirepp” (under no. 253).

Ficus prolixa Forster, Prodr. Fl. Ins. Austral. 77 (1786).

Ficus prolixoides Warburg in Fedde, Rep. Nov. Spec. i. 79 (1905).—
Synon. nov.

E r o m a n g a : Dillon Bay, alt. 300 m., rain-forest, common, no. 273, May 17, 1928 (giant Banyan of many trunks and roots; fruit black when ripe). *T a n n a* : Lenakel, alt. 100 m., rain-forest, common, no. 29, Feb. 21, 1928 (large tree of many trunks sending down many roots, up to 25 m. high; fine shade tree); alt. 200 m., rain-forest, common, no. 113, March 6, 1928 (largest Banyan on Tanna). *A n e i t y u m* : Anelgauhat Bay, sea level, rain-forest, common, no. 900, March 15, 1929 (large spreading Banyan, 18 m. high; fruit 10 mm. long, 8 mm. in diam., black when ripe).—Vernacular name “Nepang” (under no. 273) and “Banyan” (under nos. 29 and 900).

I cannot distinguish *F. prolixoides* Warb. from this species; the material at my disposal shows that the differences given by Warburg are not constant.

Sect. SYCIDIUM

Ficus aspera Forster, Pl. Esc. 36 (1786).

T a n n a : Lenakel, alt. 200 m., rain-forest, common, no. 49, Feb. 24, 1928 (small tree 8 m. high; fruit red when ripe); alt. 200 m., rain-forest, common, no. 103, March 5, 1928 (tree 8–12 m. high; fruit yellow, eaten by natives).

Ficus ciliata Warburg in Bot. Jahrb. xxv. 615 (1898).

A n e i t y u m : Anelgauhat Bay, sea level to 100 m. alt., rain-forest, common, no. 731, Feb. 11, 1929 (large tree 18 m. high;

fruit red when ripe, 14 mm. diam., flattened at the ends); sea level, sea shore, common, no. 788, Feb. 20, 1929 (small tree 6 m. high; fruit red when ripe, 15 mm. diam., flattened at top).

This species, which has been previously recorded only from Samoa, differs from *F. Kajewskii* Summerhayes in the larger receptacles and ciliate perianth lobes.

Ficus copiosa Steudel, Nomencl. ed. 2, 635 (1840).

Banks Group: Vanua Lava, sea level, rain-forest, common, no. 469, July 12, 1928 (small Fig 10 m. high, with fruit growing on trunk). **Tanna:** Lenakel, alt. 100 m., rich rain-forest soil, common, no. 24, Feb. 21, 1928 (tree 10–12 m. high; fruit red when ripe and growing on side of wood).

This species is also represented at Kew by New Hebridean specimens collected by Miss Cheesman and by Dr. A. Morrison. It is easily recognized by the fact that cork is formed at an early stage at both ends of the petioles but not in the middle. The specimens, in addition to agreeing with the description and the plate in King's monograph (the latter a reproduction of Roxburgh's original drawing), match the specimens collected in Amboina by C. B. Robinson and distributed by Merrill as *Ficus wassa* Roxb. In the writer's opinion these latter specimens are better referred to *F. copiosa* Steud. (*F. polycarpa* Roxb., non Jacq.). It is interesting to note from Roxburgh's own descriptions that the two species are probably allied, since apart from other features they both are said to possess a green gland in the axil of the lowest nerve on each side of the leaf. In his description of *F. polycarpa* Roxburgh likens his species in this respect to *F. laciniata*. There is, however, no *F. laciniata* either in Flora Indica or elsewhere, and a glance at the description and plate (in Wight's Icones) of *F. wassa*, with its leaves sometimes lacinate, suggests that Roxburgh originally named this species *F. laciniata* and afterwards changed the name to *F. wassa* forgetting, however, to make the corresponding alteration in his manuscript under *F. polycarpa*.

F. copiosa and *F. wassa* are put into different groups by Roxburgh on account of the receptacles being borne differently, but as *F. copiosa* may have its receptacles either axillary or on the older branches or trunk Roxburgh's segregation can scarcely be maintained on the original grounds alone.

For the moment, however, the descriptions and plates differ too much in other respects to justify uniting the two species. Merrill's identification of Robinson's specimens as *F. wassa* depends to a great extent on the identity of the native name given to the plants described by Rumphius and Roxburgh with that

given to Robinson's plant. Until we know, however, that the names "wassa" and "giho" are applied by the natives to one species of Fig only, we cannot be sure of the identity of the species concerned.

I am, therefore, maintaining the name *F. copiosa* Steud. for the present species, although if the two species were united *F. wassa* would have to be adopted in view of its priority.

Ficus Kajewskii Summerhayes, sp. nov.

Arbor parva, 10–15 m. alta. Ramuli teretes, graciles, leviter flexuosi, primo scabridulo-pilosi, demum glabri cortice brunneo vel cinereo-brunneo longitudinaliter ruguloso obtecti. Folia pro genere parva, petiolata, oblique ovata, oblongo-ovata, oblongo-lanceolata vel lanceolata, apice breviter obtuse vel rarius subacute acuminata, basi inaequaliter cuneata usque subcordata, usque 11 cm. longa et 5 cm. lata sed saepius satis minora, chartacea vel rarius subcoriacea, utrinque asperula, glabra, costa supra prominula subtus prominente, nervis lateralibus utrinsecus 4–6 curvatis subtus prominentibus juxta marginem arcuatim conjunctis, nervis tertiariis prominulis, rete venularum quadrato manifesto; petiolus gracilis vel subgracilis, 4–8 mm. longus, primo scabridule pilosus demum glaber, supra canaliculatus; stipulae lanceolatae, acutae, 2–3 mm. longae, extra adpresse pilosae vel fere glabrae. Receptacula axillaria, solitaria vel gemina, pedunculata, globosa vel subglobosa, 5–6 mm. longa, 6–8 mm. diametro, breviter scabrido-pilosula vel fere glabra, ostiolo parvo bracteis vix prominentibus, intus inter flores setis brevibus hyalinis numerosis instructa; pedunculus gracilis, 2–6 mm. longus, scabrido-pilosulus. supra medium vel apice bracteis tribus ovatis obtusis instructus. Flores ♀ sessiles vel rarius usque 1 mm. pedicellati, perianthii segmentis 4–5 lineari-oblongis vel oblongis obtusis vel subacutis superne ± coalitis ovarium includentibus glabris; ovarium sessile, 1–1.5 mm. longum, complanatum, obovoidem vel ellipsoideum, stylo laterali 0.6–1.2 mm. longo, stigmate minuto leviter dilatato. Flores ♂ et ♀ cecidiophori non visi.

E f a t e : Undine Bay, alt. 200 m., rain-forest, common, no. 216, April 27, 1928 (tree about 15 m. high; fruit red when ripe); Mt. McDonald, alt. 500 m., rain-forest, common, no. 233, April 28, 1928 (tree 15 m. high). E r o m a n g a : Dillon Bay, centre of island, alt. 400 m., rain-forest, common, no. 343, June 1, 1928 (small fig, 10 m. high, with very small straight trunk). A n e i - t y u m : Anelgauhat Bay, alt. 34 m., rain-forest, common, no. 737 (type), Feb. 12, 1929 (small tree 10 m. high; leaves dark

green, midrib light yellow; fruit purple black when ripe).—Vernacular name "Neme-sue" (under no. 343).

The nearest relative of this species seems to be *F. Barclayana* Summerhayes, comb. nov. (*Covellia Barclayana* Miq., *Ficus Barclayi* Seem.), a native of Fiji. Although that species is placed by Miquel in sect. *Covellia* and the female flowers are drawn as possessing no perianth, *F. Barclayana* seems to me to belong more properly to sect. *Sycidium*. Seemann's dissections from specimens which seem identical with the type show the female flowers as possessors of typical *Sycidium* perianths. *F. Kajewskii* differs from the Fiji plant in its less hairy receptacles, which are however furnished with colorless setae inside, in the perianth being quite glabrous and in minor characters of the leaves. Both species have the rough leaves and the small rough axillary receptacles characteristic of sect. *Sycidium*.

Ficus trichoneura Summerhayes, sp. nov.

Arbor parva vel mediocris usque 15 m. alta; ramuli hornotini ± adpresse hirsuti, annotini glabrescentes, cortice leviter longitudinaliter sulcato castaneo-brunneo obtecti. Folia alterna, longiuscule petiolata, rhombeo- vel oblongo-elliptica vel ovata, superne late acutata apice ipso emarginato-obtusa, basi rotundata vel subrotundata, 5–14 cm. longa, 2–6 cm. lata, chartacea, supra glabra, laevia, siccitate griseo-viridia, subtus costa et nervis primariis praesertim infimis adpresse hirsutis demum glabrescentibus, ceterum glabra, pallide viridia, saepius albedo-punctulata, costa et nervis supra prominulis subtus prominentibus, nervis primariis utrinsecus 8–10 infimis angulo acuto ceteris angulo circiter 60° e costa exeuntibus prope marginem arcuato-conjunctis, rete venularum crebro distincto; petiolus gracilis, 1–4 cm. longus, supra leviter canaliculatus, primo dense adpresse hirsutus, demum glabrescens; cortice ei caulis simili obtectus; stipulae lineari-lanceolatae, acutissimae, glabrae, castaneo-brunneae, cito deciduae. Receptacula axillaria, solitaria vel saepius gemina, alia flores ♂ et ♀ cecidiophoros, alia flores ♀ includentia, pedunculata, sphaeroidea vel subsphaeroidea, viridia, 6–7 mm. longa, 7–9 mm. diametro, glabra, umbilico prominente, ostiolo depresso, bracteis vix obviis, intus setis paucis longiusculis inter flores instructa; pedunculus falsus (stipes receptaculi) gracilis, 1–4 mm. longus, puberulus, basi bracteis tribus parvis ovatis obtusis 1 mm. longis instructus, pedunculo vero simili 0.5–5 mm. longo, totus pedunculus 4–8 mm. longus. Flores ♂ prope ostiolum, sessiles, perianthii segmentis 3–4 liberis lineari-lanceolatis antheram includentibus brunneis glabris; stamen 1, filamentum antherae aequilongo. Flores

♀ cecidiophori sessiles, brunnei, perianthio irregulariter fisso segmentis saepius 2-3 lanceolatis ovario aequilongis glabris; ovarium compresse ellipsoideum vel ovoideum, circiter 1 mm. longum, stylo laterali brevi, stigmatе breviter clavato. Flores ♀ sessiles, brunnei, perianthii segmentis tribus linearibus 1.25-5 mm. longis; ovarium compresse reniforme, 1.5 mm. longum, rugulosum, stylo laterali, stigmatе clavato ovarium paulo superante, bractea basali spathulato-lineari.

Banks Group: Vanua Lava, sea level, rain-forest, common, no. 417, July 6, 1928 (medium sized tree up to 15 m. high), and no. 426 (type) July 6, 1928 (small tree up to 6 m. high). **Eromanga:** Dillon Bay, sea level, rain-forest, common, no. 264, May 17, 1928 (smaller type of Fig averaging 10 m. high). **Tanna:** Lenakel, alt. 200 m., rain-forest, common, no. 89, March 5, 1928 (large tree 20 m. high); alt. 100 m., rain-forest soil, common, no. 23, Feb. 21, 1928 (tree 12-15 m. high; leaves dark green). **Aneityum:** Anelgauhat Bay, sea level, rain-forest, common, no. 711, Feb. 9, 1929 (Fig tree growing 20 m. high; fruit green when ripe, 6 mm. in diam.).—Vernacular name "Bongnute" (under no. 264).

This species is apparently one of the commonest Figs in the New Hebrides, as in addition to the above gatherings there are at Kew several more from the southern islands of the group. According to Miss L. E. Cheesman the species is also found in Malekula, which is quite probable, although I have not seen a specimen from that island. The species has been collected up to 300 m. altitude. There is also a specimen at Kew collected by Kajewski in the Santa Cruz Islands.

F. trichoneura is most closely allied to *F. chrysolaena* K. Schum., a native of New Guinea and the Solomon Islands, which differs in having the veins more hairy below while the lamina is also partly hairy, the receptacles larger and shortly pubescent, and the bracts immediately at the base of the receptacles so that there is no stipe. It is also interesting to note that our species very strongly resembles *F. adenosperma* Miq. which, however, by virtue of its hermaphrodite flowers is placed in sect. Palaeomorphe. Since both *F. trichoneura* and *F. chrysolaena* vary considerably from the normal type of sect. Sycidium it is possible that they are really types of sect. Palaeomorphe in which the hermaphrodite flowers have been lost. In this connection it is worthy of notice that in *F. adenosperma* wholly male flowers are present as well as hermaphrodite and gall flowers, the hermaphrodite flowers containing a properly developed gall ovary and an abortive stamen.

Sect. COVELLIA

Ficus verrucosa Vahl, Enum. II. 192 (1806).

Ficus septica Forster, Prodr. Fl. Ins. Austral. 76 (1786).—Non Burm. f.

Ficus casearia F. v. Mueller apud Bentham Fl. Austral. VI. 177 (1873).—
Summerhayes in Jour. Arnold Arbor. x. 148 (1929).

Eromanga: Dillon Bay, alt. 300 m., rain-forest, common, no. 271, May 17, 1928 (Fig with single stem up to 15 m. high; leaves dark glossy green; fruit yellow when ripe). **Aneityum**: Anelgauhat Bay, sea level, rain-forest, common, no. 793, Feb. 20, 1929 (large tree 12 m. high; fruit 12 mm. long, flattened at both sides, cream-color when ripe).—Vernacular name "Ubariherhon" (under no. 271).

This species is widely spread from the New Hebrides to New Guinea and Australia. There are specimens at Kew from the Admiralty and Solomon Islands. It is closely allied to *F. leucantoma* Poir.

Sect. EUSYCE

Ficus Moseleyana King in Ann. Bot. Gard. Calcutta, I. 144, t. 181 (1888).

Banks Group: Vanua Lava, sea level, sea shore, common, no. 433, July 7, 1928 (medium tree up to 15 m. high).

Previously known only from eastern Malaya.

Artocarpus incisa Linnaeus f., Suppl. 411 (1781).

Eromanga: Dillon Bay, common in rain-forest at sea level, no. 394, June 9, 1928 (large tree up to 20 m. high; the most useful tree of the islands as it supplies large quantities of fruit and the wood is used for canoes).—Also New Caledonia, Samoa, Society, Ellice, Gilbert, Marshall, Caroline, Mariana, Santa Cruz, Solomon, Bismarck and Admiralty Islands, New Guinea and Hawaii.—Vernacular name "Ne-marl."

URTICACEAE

Laportea crenulata (Roxb.) Gaudichaud in Arch. Mus. Nat. Paris, IX. 133, t. 2c, fig. 5 (1856).

Banks Group: Vanua Lava, common in rain-forest at sea level, no. 421, July 6, 1928 (large tree up to 15 m. high, leaves glossy above; bad as a stinging tree).—Also Bismarck Islands, New Guinea and Malaysia.

It seems that the plant found on Efate by Levat should be referred to this species and not to *L. photiniphylla*.

Elatostema macrophyllum Brongniart in Duperrey, Voy. Coquille 207, t. 45 (1829).

Aneityum: Anelgauhat Bay, common in rain-forest up to 450 m., no. 968 (coll. *J. P. Wilson*), Sept. 1929 (small shrub about 1.30 m. high; flowers small, white; fruit at base of flower, about 0.4 cm. in diam.; stem pithy).—Vernacular name “Ilbuvin.”

Procris pedunculata Weddell in De Candolle, Prodr. xvi. pt. i. 191 (1869).

Aneityum: Anelgauhat Bay, common in rain-forest at 300 m., no. 852, March 2, 1929 (plant up to 1 m. high; fruit with red pulp and white seeds).—Already found on Efate; also New Caledonia, Fiji, Samoa, Society, Marquesas, Marshall, Mariana, Solomon and Bismarck Islands and New Guinea.

Boehmeria anisoneura Guillaumin, sp. nov.

Arbor parva, trunco 15 cm. diam., ramis rufo-velutinis, foliis oppositis inaequalibus, uno valde asymmetrico ovato (usque ad 25 cm. \times 10 cm.), petiolo 6–8 cm. longo, altero fere symmetrice ovato (usque ad 12 cm. \times 8 cm.), petiolo circa 0.5 cm. longo, membranaceis margine a basi ad apicem dense serratis apice attenuatis vel longe acuminatis basi oblique rotundatis leviterque cordatis, nervis principalibus 3, uno in parte angustiore fere apicem attingenti, altero in parte latiore ad tertiam supremam partem vergente, secundariis a venarum exteriorum exteriori parte regulariter parallelis numerosis, a veno centrali ad partem latiore arcuatis paucis, nervis valde reticulatis, pagina superiore hispido-scabra, inferiore velutina, petiolo velutino, stipulis intrapetiolaribus lanceolatis 2–3 cm. longis tarde deciduis, extra praecipue secundum lineam longitudinaliter centralem argenteo-hispidis. Flores albi, in axillis glomerati, glomerulis circa 1 cm. diam. multifloris, bracteis glabris, ♀ perigonio ore breviter 2–3-dentato extra hirsuto ellipsoideo, ovario styloque glabris.

Aneityum: west coast, common in rain-forest up to 600 m., no. 1005 (coll. *J. P. Wilson*), Sept. 1929 (small tree to 15 cm. in diam.; flowers very small, white; fruit very small, at base of petiole).—Vernacular name “Nowau.”

A very remarkable species among those with axillary glomerules and opposite leaves. It seems nearest to *B. monticola* Bl. of Sumatra.

Boehmeria platyphylla (Buch-Ham.) D. Don, Prodr. Fl. Nep. 60 (1825).

Aneityum: west coast, common in rain-forest up to 450 m., no. 961 (coll. *J. P. Wilson*), Sept. 1929 (small tree to 15 cm. in diam.; flowers small; fruit very small).—Already found on Espiritu Santo; also New Caledonia, Australia (Queensland), Fiji, Samoa and Society Islands, New Guinea, Malaysia.—Vernacular name “Nahwai.”

Cypholophus macrocephalus Weddell in Ann. Sci. Nat. sér. 4, i. 198 (1854).

Aneityum: Anelgauhat Bay, common in rain-forest at 300 m., no. 766, Feb. 14, 1929 (shrub up to 3.60 m. high; fruit light green).—Also Fiji, Samoa and Society Islands, Moluccas and Malaysia.

Pipturus albidus (Hook. & Arn.) A. Gray apud Mann in Proc. Am. Acad. Sci. vii. 201 (1867).

Tanna: Mt. Tokosh Meru, common in rain-forest at 1000 m., no. 148, March 15, 1928 (small plant 1 m. high on crest of the mountain).—Also New Caledonia, Society Islands, New Guinea and Hawaii.

Pipturus argenteus Weddell in DeCandolle, Prodr. xvi. pt. i, 235¹⁹ (1869).

Aneityum: Anelgauhat Bay, common in rain-forest at sea level, no. 712, Feb. 9, 1929 (small tree up to 12 m. high; leaves dark green above, silvery beneath, with light pink petiole; fruit light green). *Tanna*: Lenakel, common in heavy rain-forest soil at sea level, no. 10, Feb. 20, 1928 (small tree up to 6 m. high; leaves dark green above, silvery underneath).—Already found on Aneityum, Erronan, Tanna and Efate; also Australia (Queensland, New South Wales), Fiji, Tonga, Society, Marquesas, Mariana and Bismarck Islands, New Guinea, Moluccas and Malaysia.

Pipturus repandus Weddell in Arch. Mus. Paris, viii. 448 (1855).

Tanna: Mt. Tokosh Meru, common in rain-forest at 200 m., no. 144, March 14, 1928 (tree up to 20 m. high; natives use root for cleaning hair).—Also New Caledonia, Loyalty Islands, Malaysia and Hawaii.

Leucosyke capitellata Weddell in De Candolle, Prodr. xvi. pt. i. 235²⁷ (1869).

Aneityum: west coast, common in lower forest ranges up to 180 m., no. 963 (coll. *J. P. Wilson*), Sept. 1929 (small tree, trunk up to 0.3 m. diam., flowers yellow; fruit round, brown); Anelgauhat Bay, common in rain-forest at 60 m., no. 759, Feb. 13, 1929 (small tree up to 9 m. high; leaves silvery underneath, with brown-green veins). *Efate*: Undine Bay, common in rain-forest at 300 m., no. 227, April 27, 1928 (tree up to 10 m. high; leaves green above, silvery underneath).—Also Solomon Islands (?), Bismarck Islands, New Guinea, Moluccas and Malaysia.—Vernacular name "Niicki-fig" (under no. 963).

CASUARINACEAE

Casuarina equisetifolia Linnaeus, Amoen. Acad. iv. 143 (1759).—Forster, Char. Gen. 103, fig. 52 (1776).

Aneityum: Anelgauhat Bay, common on seashore, no. 697, Feb. 4, 1929 (tall tree up to 20 m. high, common throughout the New Hebrides). *Banks Group*: Vanua Lava, common on seashore, no. 451, July 9, 1928 (tree up to 20 m. high growing on the average much larger than the Queensland coastal "She-oak").—Already found on Aniwa; also New Caledonia, Australia (Queensland, North Australia), Fiji, Tonga, Cook, Society, Marquesas, Mariana, Solomon, Bismarck and Admiralty Islands, New Guinea, Malaysia.

ORCHIDACEAE

Determined by OAKES AMES

Corymborchis veratrifolia (Reinw.) Blume, Fl. Jav. nov. ser. i. 105, t. 43, fig. 1 (1858).

Tanna: no. 146 (see p. 127).

Malaxis neo-ebudica Ames in Jour. Arnold Arb. XIII. 128 (1932).

Tanna: no. 137 (see p. 128).

Malaxis xanthochila (Schltr.) Ames & Schweinfurth in Ames, Orch. vi. 73 (1920).

Aneityum: no. 837 (see p. 128).

Liparis condylobulbon Reichenbach f. in Hamb. Gartenz. XVIII. 34 (1862).

Eromanga and *Banks Group*: nos. 321 and 455 (see p. 129).

Dendrobium (§ *Aporum*) sp.

Efafe: no. 190 (see p. 131).

Eria Kajewskii Ames in Jour. Arnold Arb. XIII. 135 (1932).

Aneityum: no. 820 (see p. 135).

Ceratostylis subulata Blume, Bijdr. 306 (1825).

Efafe: no. 234 (see p. 138).

Earina Brousmichei Kränzlin in Lecomte Not. Syst. iv. 136 (1928).

Aneityum: no. 844 (see p. 138).

Appendicula reflexa Blume, Bijdr. 301 (1825).

Aneityum and *Eromanga*: nos. 915 and 326 (see p. 138).

Spathoglottis Petri Reichenbach f. in Gard. Chron. n. ser. VIII. 392 (1877).

Eromanga: no. 306 (see p. 140).

Saccolabium Kajewskii Ames in Jour. Arnold Arb. XIII. 141 (1932).
E f a t e and *B a n k s* G r o u p: nos. 205 and 448 (see p. 141).

ZINGIBERACEAE

Zingiber zerumbet Roscoe apud Smith, Exot. Bot. II. 105, t. 112 (1805); in Trans. Linn. Soc. VIII. 348 (1807).

A n e i t y u m: Anelgauhat Bay, common in rain-forest at 180 m., no. 850, March 2, 1929 (plant up to 1.5 m. high; flowers white).—Also New Caledonia, Australia (Queensland), Fiji, Samoa, Society, Marquesas, Mariana and Bismarck Islands, New Guinea, Malaysia and Hawaii.

Alpinia Blumei K. Schumann in Bot. Jahrb. XXVII. 282 (1900) ?

B a n k s G r o u p: Vanua Lava, common in rain-forest at sea level, no. 416, July 5, 1928 (tall plant about 3 m. high, along water courses; flowers bright pink).

The characters agree well with the description of this Javanese species except that the inflorescence attains 14 cm., but the flowers are lacking and it is impossible to know the shape of the bractlet. In any case the plant belongs in the genus *Guillainia*.

MARANTACEAE

Donax arundastrum Loureiro, Fl. Coch. 11. (1790).

B a n k s G r o u p: Vanua Lava, common in swampy rain-forest at sea level, no. 420, July 6, 1928 (plant up to 2 m. high with branches radiating from one node; flowers white to cream-colored; fruit 1.5 cm. in diam.).—Also in the Philippines and Asia.

AMARYLLIDACEAE

Crinum pedunculatum R. Brown, Prodr. Fl. Nov. Holl. 297 (1810).

A n e i t y u m: Anelgauhat Bay, common along sea shore, no. 805, Feb. 21, 1929 (large plant up to 1.5 m. high, growing close to the beaches; leaves numerous, long; flowers white).—Also New Caledonia, Australia (Queensland, New South Wales, South Australia), Tonga and Cook Islands, New Guinea, Moluccas and Malaysia?

TACCACEAE

Tacca pinnatifida Forster, Gen. Char. 70, t. 35 (1776).

E r o m a n g a: Dillon Bay, common in rain-forest at 400 m., no. 345, June 1, 1928 (plant up to 80 cm. high growing wild on all the islands; arrowroot is manufactured from the bulbs and has been a source of revenue for the mission stations).—Also New Caledonia, Loyalty Islands, Australia (Queensland, South Australia),

Fiji, Tonga, Samoa, Society, Marquesas, Ellice, Marshall, Caroline, Mariana, Solomon and Bismarck Islands, New Guinea, Malaysia and Hawaii.—Vernacular name “Yovoli.”

DIOSCOREACEAE

Dioscorea bulbifera Linnaeus, Sp. Pl. 1033 (1753).

A n e i t y u m : Anelgauhat Bay, common in rain-forest at sea level, no. 896, March 11, 1929 (wild yam growing over the small trees; not edible).—Already found on Efate; also New Caledonia, Loyalty Islands, Australia (Queensland), Fiji, Tonga, Samoa, Society, Marquesas, Caroline and Mariana Islands, New Guinea, Moluccas, Malaysia and Hawaii.

Dioscorea nummularia Lamarck, Encyc. Méth. III. 231 (1789). ?

E r o m a n g a : Dillon Bay, common in native gardens, rain-forest at sea level, no. 250, May 15, 1928 (climbing on sticks placed by natives who take great care of its cultivation; this red yam is the chief food of natives).—Also Australia (Prince of Wales Island), Fiji, Society, Caroline and Bismarck Islands, New Guinea, Moluccas, Philippines.—Vernacular name “Loop.”

It is strange that the collector indicates *D. nummularia* as the edible species and *D. bulbifera* as the wild species, and one may ask whether the labels have not been interchanged.

LILIACEAE

Smilax vitiensis A. De Candolle in De Candolle, Monogr. Phaner. I. 204 (1878).

B a n k s G r o u p : Vanua Lava, common in rain-forest at 500 m., no. 483, July 16, 1928 (vine growing over rain-forest trees; fruit purple to black when ripe).—Also Fiji and Bismarck Islands.

Smilax sp.

A n e i t y u m : Anelgauhat Bay, common in rain-forest at 210 m., no. 819, Feb. 28, 1929 (vine growing over rain-forest trees; fruit 1.3 cm. long, 1.5 cm. in diam., black when ripe).

Geitonoplesium cymosum A. Cunningham in Bot. Mag. t. 3131 (1832).

A n e i t y u m : Anelgauhat Bay, common in rain-forest at sea level, no. 832, Feb. 28, 1929 (vine growing over rain-forest trees; fruit 0.5 cm. long, 0.8 cm. in diam., black when ripe).—Also New Caledonia, Loyalty Islands, Australia (Queensland, New South Wales, Victoria), Norfolk Island, Fiji and Bismarck Islands and New Guinea.

Dianella ensifolia [A. P. DeCandolle in] Redouté, Lil. 1. 1, t. 1 (1802).

Eromanga: Dillon Bay, common in poor red soil, open country at 400 m., no. 346, June 1, 1928 (plant about 1 m. high; flowers pale blue).—Also New Caledonia, Australia (Queensland, North Australia), Fiji, Tonga, Society, Caroline and Mariana Islands, New Guinea, Malaysia and Hawaii.—Vernacular name "Did-and-Did."

Dracaena sp.

Aneityum: Anelgauhut Bay, common in rain-forest at sea level, no. 881, March 6, 1929 (up to 6 m. high; fruit 2.5 cm. long, 3 cm. in diam.; black when ripe; leaves used for making grass skirts).

The leaves of the plant resemble exactly those of *D. aurantiaca* Wall. of the Philippines and Asia.

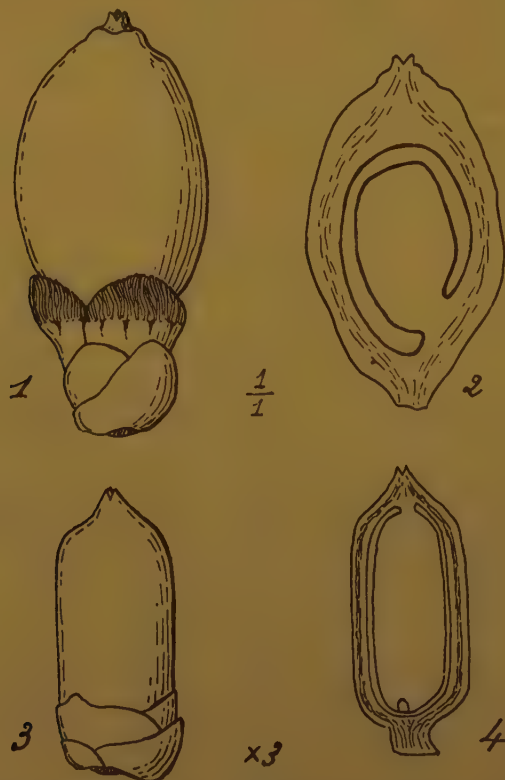


FIG. 1.—*CHAMBEYSRENIA* sp.: 1. Fruit. 2. Longitudinal section of fruit. *CYPHOPHOENIX* sp.: 3. Fruit. 4. Longitudinal section of fruit.

PALMAE

Chambeyronia sp. aff. *C. macrocarpa* Vieill.

Fig. 1: 1, 2

Banks Group: Vanua Lava, rare in rain-forest at sea level, no. 428, July 6, 1928 (Palm up to 15 m. high; fruit edible).

Cyphophoenix sp. nov. ?

Fig. 1: 3, 4

Banks Group: Vanua Lava, common in rain-forest at 100 m., no. 465, July 11, 1928 (tall palm 15 m. high; fronds about 2 m. long).

The fruit resembles completely that of *C. elegans* H. Wendl. of New Caledonia, the only species of the genus, but differs in its smaller size (1.8 cm. \times 0.4 cm.), its turbinate shape and its smooth pericarp.

Kajewskia aneityensis Guillaumin, gen. nov. et sp. nov. Fig. 2

Palma 20 m. alta, foliis ultra 4 m. longis pinnatisectis, segmentis lanceolatis (circa 60 cm. \times 8 cm.) acuminatis in axilla subtusque ad costae basin brunneo-filamentoso-squamatis. Spadix valde

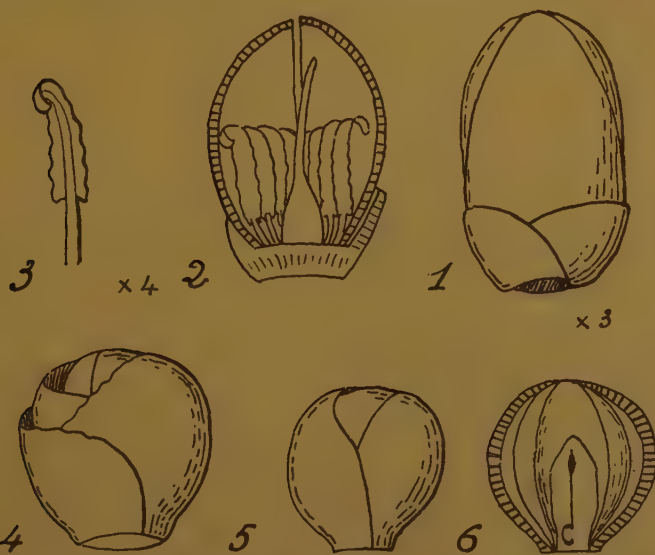


FIG. 2.—*KAJEWSKIA ANEITYENSIS* Guillaumin: 1. Staminate flower. 2. Longitudinal section of staminate flower. 3. Stamen. 4. Pistillate flower. 5. Corolla. 6. Longitudinal section of pistillate flower.

ramosus, ramis angulosis brunneo-squamatis, floriferis circa 15 cm. longis valde sinuosis, floribus ♂ et ♀ intermixtis singulis vel 2-nis uno ♂ altero ♀, ♂ ellipsoideis (12 mm. \times 7 mm.) vertice rotunda-

tis symmetricis, sepalis rotundatis ad 4 mm. longis imbricatis, petalis ellipticis apicem versus attenuatis crassis valvatis, staminibus ∞ , antheris linearibus apice recurvis undulatis 4 mm. longis, loculis parallelis basi leviter divaricatis, filamentis duplo brevioribus connectivo nigro continuis, pistillodio basin versus incrassato in collum tenuem attenuato stamina superante, ♀ globosis (8 mm. diam.), sepalis laxis valde imbricatis ad 8 mm. longis ovato-rotundatis, petalis inclusis valde appresse cucullato intricatis 7 mm. longis ovato-rotundatis, staminodiis 0, ovario oblonge turbinato tertia suprema parte conice stigmatoso, ovulo 1 parietali ad loculi basin inserto.

Aneityum: Anelgauhat Bay, not common in rain-forest at sea level, no. 784, Feb. 19, 1929 (large palm to 18 m. high; fronds up to 3.5 m. long; stamens white, anthers cream-colored).

Near *Actinokentia*, a genus represented only by *A. divaricata* Dammer (= *A. Schlechteri* Dammer) of New Caledonia, but differs in its much larger flowers resembling those of *Arenga*, not regularly arranged in three's (2 lateral and 1 central flower) and in the absence of the staminodes in the pistillate flower.

PANDANACEAE

Determined by U. MARTELLI

Pandanus Cominsii Hemsley in Hooker's Icon. Pl. xxvii. t. 2654 (1900).

Banks Group: Vanua Lava, common in rain-forest at 100 m., no. 471, July 12, 1928 (up to 4 m. high, much smaller than its coastal relative; fruit red when ripe, on a cylindrical spike).—Also found in Solomon Islands.

Freycinetia tannaensis Martelli in Jour. Arnold Arb. xii. 269 (1930).

Plate 43

Tanna: on Mt. Tokosh Meru, very common in rain-forest, at 800 m., no. 163, March 15, 1928 (climbing up the trunks of trees).

ARACEAE

Epipremnum pinnatum (L.) Engler in Engler, Pflanzenr. iv. 23^b, p. 60 (Arac.) (1908).

Aneityum: Anelgauhat Bay, common in rain-forest at 210 m., no. 830, Feb. 28, 1929 (climbing up the trunks of trees: fruit 10–15 cm., long).—Already found on Tanna; also in New Caledonia, Loyalty Islands, Australia (Queensland), Fiji, Tonga, Marshall and Bismarck Islands, New Guinea, Moluccas and Malaysia.



FREYCINETIA TANNAENSIS Martelli
Photograph of type in the Herbarium Martelli

CYPERACEAE¹

Pycreus polystachyus Beauvais, Fl. Owar. II. 48, t. 86 (1807).

Eromanga: Dillon Bay, common in cleared rain-forest at sea level, no. 277, May 19, 1928 (small sedge 30–40 cm. high).—Also New Caledonia, Australia (Queensland, New South Wales), Samoa, Cook and Bismarck Islands, New Guinea, Malaysia.—Vernacular name “Overi-car.”

Kyllingia monocephala Rottboell, Descr. Ic. 13, t. 4, fig. 4 (1773).

Eromanga: Dillon Bay, commonly growing in cleared rain-forest at sea level, no. 276, May 19, 1928 (sedge 25–40 cm. high; macerated with leaves of “Denyung” (Cane grass) in cold water and drunk for spleen trouble; macerated with leaves of “Naivoss,” “Tomirirri” and “Nesivinesip” (shrub) in cold water and drunk by women in state of pregnancy for good health).—Already found on Aneityum, waste place (*MacGillivray*, no. 53, December 1858 [unpublished locality]) and on Efate; also New Caledonia, Australia (Queensland, New South Wales), Norfolk Island, Fiji, Tonga, Samoa, Cook, Society, Caroline, Mariana, Santa Cruz, Solomon and Bismarck Islands, New Guinea and Malaysia.—Vernacular name “Polell.”

Fimbristylis communis Kunth, Enum. Pl. II. 234 (1837).

Eromanga: Dillon Bay, common in open grass country at 300 m., no. 318, May 28, 1928 (sedge about 50–75 cm. high; plaited together by women for grass dresses).—Already found on Aneityum, swamp (*MacGillivray*, no. 24, Oct. 1858 [unpublished locality]).—Also New Caledonia, Australia (Queensland, New South Wales, North Australia), Tonga, Cook, Society, Mariana and Bismarck Islands, New Guinea and Malaysia.—Vernacular name “Farll.”

Lepidosperma sp. cf. *L. elatius* Labill. of Australia (Victoria, Tasmania).

Tanna: Mt. Tokosh Meru, common in rain-forest at 1000 m., no. 155, March 15, 1928 (sedge on very top of the mountains).

Cladium Milnei C. B. Clarke in Kew Bull. Add. ser. 8, p. 46 (1908).

Eromanga: Dillon Bay, common in poor red soil, bracken country, no. 327, May 29, 1928 (about 1 m. high; seed bright brown).—Already found on Aneityum.²—Vernacular name “Did-and-did.”

¹ To the plants cited in my “Liste des plantes connues [des Nouvelles Hébrides] (in Bull. Soc. Bot. France LXXIV. 709, 1927) the following should be added: *Fimbristylis monostachya* Hassk., Aneityum, open place (*MacGillivray*, no. 44), Feb. 1859; *Scirpus mucronatus* L., Eromanga, stream (*MacGillivray*, n. 7), Sept. 1879; *Rynchospora aurea* Vahl, Aneityum, swamps (*MacGillivray*, no. 28), Oct. 1878 (inedited).

² Omitted from my “Liste des plantes connues [des Nouvelles Hébrides]. (Bull. Soc. Bot. France LXXIV. 709. 1927).

GRAMINEAE

Determined by A. S. HITCHCOCK

Isachne distichophylla Munro in Jour. Bot. VII. 178 (1869), nom. nud.; Hillebrand, Fl. Hawaiian Isl. 504 (1888).

Tanna: Mt. Tokosh Meru, common in rain-forest at 1000 m., no. 147, March 15, 1928 (small grass right on the top of Tokosh Meru).—Also in Hawaii.

Brachiaria subquadrifaria (Trin.) Hitchcock in Lingnan Sci. Jour. VII. 214 (1931).

Eromanga: Dillon Bay, common in cleared rain-forest at sea level, no. 278, May 19, 1928 (short grass 30–40 cm. high; one of the commonest grasses in the islands, growing among the cocoanuts after the scrub has been felled; the natives say it is introduced).—Also Australia (Queensland, South Australia), Mariana and Bismarck Islands.—Vernacular name “Noth-lor-si.”

Brachiaria ambigua (Trin.) A. Camus in Lecomte, Fl. Gén. Indo-Chine, VII. 433 (1922).

Eromanga: Dillon Bay, common in clearings in rain forest at sea level, no. 279, May 19, 1928 (grass about 60 cm. high; introduced).—Already found in Aneityum; also New Caledonia, Fiji, Samoa, Cook, Mariana and Solomon Islands.

Syntherisma microbachne (Presl) Hitchcock in Mem. Bishop Mus. Honolulu, VIII. 177 (1922).

Eromanga: Dillon Bay, common in rain-forest clearings at sea level, no. 280, May 19, 1928 (grass 0.60–1 m. high; cattle are not very fond of it).—Also in South America.—Vernacular name “Nof-le-fule.”

Oplismenus compositus (L.) Beauvois, Essai Agrost. 54 (1812).

Eromanga: Dillon Bay, common in rain-forest clearing at sea level, no. 281, May 19, 1928 (grass about 80 cm. high in the scrub).—Already found on Aneityum, Epi and Espiritu Santo; also New Caledonia, Loyalty, Fiji, Society, Gambier and Marquesas Islands and Hawaii.—Vernacular name “Nooh-nempeli.”

Cenchrus calyculatus Cavanilles, Ic. v. 39. t. 463 (1799).

Eromanga: Dillon Bay, common in rain-forest at sea level, no. 358, June 4, 1928 (tall grass about 1.25 m. high; seeds troublesome to clothing).—Already found on Espiritu Santo; also New Caledonia, Loyalty, Fiji, Cook, Society, Gambier, Caroline and Mariana Islands and Hawaii.—Vernacular name “Ularhai.”

Coix lacryma-jobi Linnaeus, Sp. Pl. 972 (1753).

Tanna : Lenakel, common in rain-forest clearings at 200 m., no. 118, March 6, 1928 (weed in native gardens).—Already found on Tanna; also New Caledonia, Queensland, Fiji, Tonga, Samoa, Society, Marshall, Solomon, Bismarck Islands, New Guinea and Malaysia.

Miscanthus sinensis Andersson in Oefv. Svensk. Vetensk.-Akad. Stockh. 1855, p. 166.

Tanna : Lenakel, common in rain-forest soil at 100 m., no. 39, Feb. 22, 1928 (tall cane 4–6 m. high; used by natives for arrows and roofs of houses).—Already found in Aneityum; also New Caledonia, Fiji, Tonga, Cook, Society Island and Malaysia.

Centotheca latifolia Trinius, Fund. Agrost. 141 (1820).

Eromanga : Dillon Bay, common in semi-cleared rain-forest at sea level, no. 338, May 29, 1928 (chewed by natives and applied to burns).—Already found in Aneityum and Tanna; also New Caledonia, Australia (Queensland, North Australia), Fiji, Tonga, Samoa, Cook, Society, Marquesas, Caroline, Mariana, Bismarck and Admiralty Island, New Guinea and Malaysia.—Vernacular name "Now-now."

CONIFERAE

Podocarpus imbricatus Blume, Enum. Pl. Javae, 89 (1827).

Podocarpus cupressinum R. Brown apud Mirbel in Mém. Mus. Hist. Nat. Paris, xiii. 75 (Geogr. Conif.) (1825), nomen.—R. Brown apud Bennett, Pl. Jav. Rar. 25, t. 10 (1838–52).

Aneityum : Anelgauhat Bay, common in rain-forest at 150 m., no. 849, Aug. 2, 1929 (up to 12 m. high; seed about 1 cm. long, 1 cm. in diam. resting on a fleshy growth 0.5 cm. long).—Already found on Aneityum; also Fiji Islands, Malaysia and Philippines.

Agathis obtusa (Lindl.) Masters in Jour. Roy. Hort. Soc. Lond. xvi. 197 (1892).

Aneityum : Anelgauhat Bay, common in rain-forest at 150 m., no. 706, Feb. 5, 1929 (large tree up to 40 m. high on well drained slopes where the soil is intensely volcanic and red, especially typical of the country where the Kauri is found on the islands; this specimen is remarkable for the small size of the cones and the irregular sunken places on their surface; the best timber tree for boat building in the southern hemisphere); common in rain-forest at 60 m., no. 760, Feb. 13, 1929 (giant tree; cones malformed); common in rain-forest at 100 m., no. 707, Feb. 19, 1929.—Already found on Aneityum and Eromango.—Determined by E. H. Wilson.

CYCADACEAE

Cycas circinalis Linnaeus, Sp. Pl. 1188 (1753).

Eromanga: Dillon Bay, common in rain-forest and open country at 300 m., no. 400, June 8, 1928 (Cycad up to 10 m., high; fronds up to 2 m. long; fruit yellow, borne in fours).—Already found in the New Hebrides; also New Caledonia, Loyalty Islands, Australia (North Australia), Fiji, Tonga, Caroline, Mariana, Solomon, Bismarck and Admiralty Islands, New Guinea, Malaysia.—Ver-nacular name "No-mall."

This is perhaps the same species as that named *C. neo-caledonica*, by Linden (without description).

PTERIDOPHYTA

DETERMINED BY E. B. COPELAND

HYMENOPHYLLACEAE

Trichomanes Boryanum Kunze, Farnkräuter, 237 (1847).

Aneityum: Anelgauhat Bay, common in rain-forest at 150 m., no. 883, March 7, 1929 (about 15 cm. high). **Banks Group:** Vanua Lava, common in rain-forest at 400 m., in rain-forest where the rain-fall reaches 250 inches per annum, no. 461, July 10, 1928.

Trichomanes Bauerianum Endlicher, Prodr. Fl. Norf. 17 (1833).

Aneityum: Anelgauhat Bay, common in gullies in rain-forest at 600 m., no. 864, March 5, 1929 (growing in shade at high altitudes). **Tanna:** Mt. Tokosh Meru, common in rain-forest at 800 m., no. 164, March 15, 1928.

Trichomanes meifolium Bory apud Willdenow, Spec. Pl. V. 509 (1810).

Aneityum: Anelgauhat Bay, common in rain-forest moun-tains at 750 m., no. 867, March 5, 1929.

Trichomanes sp.

Banks Group: Vanua Lava, common on mountains in rain-forest at 300 m., where the rain-fall reaches about 250 inches per annum, no. 454, July 12, 1928.

The specimen which is sterile may belong to *T. aphlebioides* Christ.

Hymenophyllum formosum Brackenridge in Bot. Wilkes U. S. Expl. Exp. xvi. 268, t. 32, fig. 3 (1854).

Aneityum: Anelgauhat Bay, common in rain-forest at 750 m., nos. 868 and 871^a, March 5, 1929 (small fern growing upon rain-forest trees).

CYATHEACEAE

Balantium, an *B. dubium*?

Aneityum: Anelgauhat Bay, common in rain-forest at 150 m., no. 885, March 9, 1929 (large tree fern; trunk up to 1.5 m. high; fronds up to 2.8 m. long).

Balantium stramineum (Labill.) Diels in Engler & Prantl, Nat. Pflanzenfam. I.-4, p. 119 (1899).

Aneityum: Anelgauhat Bay, common in rain-forest at 210 m., no. 859, March 4, 1929 (fronds up to 2.8 m. long; main stem growing close to the ground).

Cyathea laciniata Copeland in Univ. Calif. Publ. Bot. xii. 389 (1931).

Aneityum: Anelgauhat Bay, common in rain-forest at 600 m., no. 876, March 5, 1929 (small tree fern up to 3.1 m. high; fronds up to 1.5 m. long).

Cyathea leucolepis Mettenius in Ann. Mus. Bot. Lugd.-Bat. i. 56 (1863).

Aneityum: Anelgauhat Bay, common in rain-forest at 210 m., no. 861, March 4, 1929 (tree fern up to 6 m. high; fronds up to 3 m. long).

Cyathea medullaris (Forst.) Swartz in Jour. Bot. Schrad. 1800, pt. ii. 94 (1801).

Aneityum: Anelgauhat Bay, common in rain-forest up to 210 m., no. 857, March 4, 1929 (tree fern up to 9 m. high; fronds up to 3 m. long). *Tanna*: Lenakel, common in rain-forest at 150 m., no. 54, Feb. 24, 1928 (tree fern up to 8 m. high; fronds 3-3.5 m. long).

POLYPODIACEAE

Dryopteris rubrinervis (Mett.) Christensen, Ind. Fil. 289 (1905).

Tanna: Lenakel, common in rain-forest soil at 200 m., no. 61, Feb. 24, 1928 (large fern in gullies; fronds about 2 m. long).

Probably identical with *D. urophylla* Christens.

Dryopteris urophylla (Wall.) Christensen, Ind. Fil. 299 (1905).

Aneityum: Anelgauhat Bay, common in rain-forest at 210 m., no. 858, March 4, 1929 (large fern; trunk small at base up to about 0.3 m. high; fronds up to 2.1 m. long).

Dryopteris sp.

Aneityum: Anelgauhat Bay, common in rain-forest at 210 m., no. 860, March 4, 1929 (main stem not more than 0.3 m. high; fronds up to 2.1 m. long).

Dryopteris sp.

Tanna : Lenakel, common in heavy rain-forest at sea level, no. 5, Feb. 20, 1929 (fern growing in clumps, 0.6–1 m. high).

Dryopteris sp.

Tanna : Lenakel, common in heavy rain-forest at sea level, no. 5, Feb. 20, 1928 (fern growing in clumps, 0.6–1 m. high).

Polystichum aristatum (Forst.) Presl, Tent. Pterid. 83 (1863).

Aneityum : Anelgauhat Bay, common in dense shade in rain-forest at 300 m., no. 847, March 2, 1929 (fronds up to 1 m. long).

Campium lonchophorum (Kunze) Copeland, comb. nov.

Acrostichum lonchophorum Kunze, Farnkräuter, pl. 2 (1840).

Aneityum : Anelgauhat Bay, common in rain-forest at 450 m., no. 893, March 9, 1929 (fronds up to 0.60 m. long).

Dipteris conjugata Reinwardt in Syll. Pl. Ratisb. II. 3 (1824).

Aneityum : Anelgauhat Bay, common on banks of rain-forest streams at 150 m., no. 916, March 17, 1929. **Eromanga** : Dillon Bay, common in rain-forest at 400 m., no. 325, May 29, 1928 (growing in clumps, about 60 cm. high).—Vernacular name “Nenn-parr” (under no. 325).

Oleandra ciliata Klotzsch apud Kuhn in Linnaea, xxxvi. 126 (1869).

Aneityum : Anelgauhat Bay, common at 750 m., no. 874, March 5, 1929 (fern climbing up trees; stem dark brown).

Humata pusilla (Mett.) Carruthers in Seemann, Fl. Vit. 335, (1873).

Aneityum : Anelgauhat Bay, common in rain-forest at 150 m., no. 855, March 4, 1929 (small climbing fern just appearing outside the moss on trees).

Davallia solida Swartz in Jour. Bot. Schrad. 1800, pt. II. 87 (1801).

Aneityum : Anelgauhat Bay, common in rain-forest at sea level, no. 835, March 1, 1929 (fern with an underground rhizome, sometimes growing on the trunks of trees).

Microlepia speluncae (L.) Moore, Ind. Fil. xciii. (1857).

Tanna : Lenakel, common in heavy rain-forest soil at sea level, no. 6, Feb. 20, 1928 (80 cm. to 1.25 m. high).

Tapeinidium tenue (Brack.) Copeland in Bernice P. Bishop Mus. Bull. LIX. 69 (1929).

Aneityum : Anelgauhat Bay, common in rain-forest at

150 m., no. 894, March 9, 1929 (fern growing on ground; fronds up to 0.6 m. long).

Dennstaedtia samoensis (Brack.) Moore, Ind. Fil. 307 (1861).

Aneityum: Anelgauhat Bay, common in rain-forest at 150 m., no. 884, March 9, 1929 (tree fern with small trunk about 0.45 m. high; fronds up to 3 m. long).

Lindsaya decomposita Willdenow, Sp. Pl. v. 425 (1810).

Banks Group: Vanua Lava, common in rain-forest at 700 m., no. 458, July 10, 1928.

Athyrium accedens (Bl.) Milde in Bot. Zeit. 1870, p. 353.

Tanna: Lenakel, common in rain-forest at 150 m., no. 133, March 8, 1928 (about 1 m. high).

Athyrium sp.

Aneityum: Anelgauhat Bay, common in rain-forest at 600 m., no. 877, March 5, 1929 (tree fern about 2.5 m. high; fronds up to 2 m. long).

Athyrium sp.

Tanna: Lenakel, common in rain-forest soil at 200 m., no. 55, Feb. 24, 1928 (large fern; fronds about 2-2.5 m. long).

Asplenium affine Swartz in Jour. Bot. Schrad. 1800, pt. II. 56 (1801).

Aneityum: Anelgauhat Bay, common in rain-forest at 150 m., no. 888, March 9, 1929 (fern growing on trees or on the ground; fronds 1 m. long).

Asplenium amboinense Willdenow, Sp. Pl. v. 303 (1810).

Aneityum: Anelgauhat Bay, common in rain-forest at 210 m., no. 838, March 2, 1929 (small-leaved fern growing on small trees in dense shade).

Asplenium brachycarpum (Mett.) Kuhn in Linnaea, xxxvi. 104 (1869).

Aneityum: Anelgauhat Bay, common in rain-forest at 600 m., no. 878, March 5, 1929 (small tree fern up to 1.5 m. high; trunk 45 cm. high; fronds up to 1 m. long).

Asplenium laserpitiifolium Lamarck, Encycl. Méth. II. 310 (1786).

Aneityum: Anelgauhat Bay, common in rain-forest at 300 m., no. 848, March 2, 1929 (fronds up to 1.5 m. long). *Tanna*: Lenakel, common in rain-forest at 100 m., no. 71, March 1, 1928 (about 1 m. high).

Asplenium nidus Linnaeus, Sp. Pl. 1079 (1753).

Banks Group: Vanua Lava, common in rain-forest at sea level, no. 444, July 12, 1928 (growing on trees, common throughout the group).

Asplenium sp.

Aneityum: Anelgauhat Bay, common in rain-forest at 300 m., no. 887, March 9, 1929 (growing sometimes on trees, sometimes on rocks; fronds up to 0.6 m. long).

Blechnum gibbum (Labill.) Mettenius in Ann. Sci. Nat. sér. 4, xv. 68 (1861).

Aneityum: Anelgauhat Bay, common in rain-forest at 210 m., no. 856, March 4, 1929 (small tree fern up to 1.5 m. high, bearing distinct sterile and fertile fronds; fronds up to 1.3 m. long).
Tanna: Ikiti, common along rain-forest streams at 100 m., no. 171, March 16, 1928 (small tree fern up to 1.5 m. high; growing in clumps with 10 or more stems in one clump).

Blechnum opacum (Baker) Mettenius in Ann. Sci. Nat. sér. 4, xv. 69 (1861).

Aneityum: Anelgauhat Bay, common in rain-forest at 600 m., no. 879, March 5, 1929 (small fern bearing distinct sterile and fertile fronds).

Blechnum Patersoni (R. Br.) Mettenius, Fil. Hort. Bot. Lips. 64, t. 4, figs. 4-10 (1856).

Tanna: Mt. Tokosh Meru, common in rain-forest at 300 m., no. 156, March 15, 1928 (about 1 m. high).

Sphenomeris chusana (L.) Copeland in Bernice P. Bishop Mus. Bull. LIX. 69 (1929).

Aneityum: Anelgauhat Bay, common in rain-forest at 180 m., no. 891, March 9, 1929 (growing on the ground; fronds up to 0.65 m. long).

Aspleniopsis decipiens Mettenius apud Kuhn, Chaetopt. 325 (1882).

Aneityum: Anelgauhat Bay, common in rain-forest at 750 m., no. 870, March 5, 1929 (small fern up to 15 cm. high).

Cheilanthes hirsuta (Poir.) Mettenius in Abhandl. Senckenb. Naturf. Ges. v. 25, n. 17 (1859).

Notholaena hirsuta (Poir.) Desvaux in Jour. de Bot. Appl. i. 93 (1813).

Aneityum: Anelgauhat Bay, common in the open along seashore at sea level, no. 928, March 17, 1929.

Adiantum aneitense Carruthers in Seemann, Fl. Vit. 346 (1873).

Aneityum: Anelgauhat Bay, common in rain-forest at 150 m., no. 889, March 9, 1929 (fronds up to 0.65 m. long).

Adiantum diaphanum Blume, Enum. Pl. Jav. 215 (1828).

Tanna: Lenakel, common on sides of gullies in rain-forest at 200 m., no. 56, Feb. 24, 1928 (very small fern).

Pteris comans Forster, Fl. Ins. Austr. Prodr. 79 (1786).

Aneityum: Anelgauhat Bay, common on banks of creeks in rain-forest at sea-level, no. 719, Feb. 9, 1929 (fronds up to 3 m. long).

Pteris ensiformis Burmann, Fl. Ind. 230 (1768).

Aneityum: Anelgauhat Bay, common in rain-forest at 150 m., no. 904, March 11, 1929 (up to 0.6m. high).

Pteris tripartita Swartz in Jour. Bot. Schrad. 1800, pt. II. 67 (1801).

Aneityum: Anelgauhat Bay, common along streams in rain-forest at 150 m., no. 892, March 9, 1929 (fronds up to 2.8 m. long).

Vittaria lineata (L.) Smith in Mem. Acad. Sci. Turin, v. 421, t. 9, fig. 5 (1793).

Aneityum: Anelgauhat Bay, common in rain-forest at 150 m., no. 934, March 17, 1929 (up to 0.3 m. high; growing on bark of trees).

Hymenolepis mucronata Fée, Gen. Fil. 82 (1850-52).

Aneityum: Anelgauhat Bay, common in rain-forest at 210 m., no. 890, March 9, 1929 (climbing upon trees).

Polypodium blechnoides (Grev.) Hooker, Sp. Fil. IV. 180 (1862).

Aneityum: Anelgauhat Bay, common in rain-forest near the summit of the mountain at 450 m., no. 886, March 9, 1929 (small fern).

Polypodium scolopendria Burmann, Fl. Ind. 232 (1768).

Eromanga: Dillon Bay, common in rain-forest at 300 m., no. 380, June 7, 1928 (small fern).—Vernacular name "Nemkar woramel."

Selliguea feeioides Copeland in Bernice P. Bishop Mus. Bull. LIX. 94 (1929).

Aneityum: Anelgauhat Bay, common in rain-forest at 750 m., no. 875, March 5, 1929 (climbing upon trees). *Tanna*:

Mt. Tokosh Meru, common in rain-forest at 800 m., no. 165, March 15, 1928 (climbing along the trunks of trees).

Cyclophorus acrostichoides (Forst.) Presl, Epimel. Bot. 130 (1849).

Aneityum: Anelgauhat Bay, common in rain-forest at sea level, no. 714, Feb. 9, 1929 (growing on tree trunks and climbing by means of runners; common throughout the islands). *Tanna*: Lenakel, common in rain-forest at 200 m., no. 101, March 5, 1928 (parasitic fern).

Drynaria rigidula (Sw.) Beddome, Ferns Br. Ind. t. 314 (1869).

Aneityum: Anelgauhat Bay, common in rain-forest at sea level, no. 834, March 1, 1929 (growing on trees; stem shielded by a brown heart-shaped growth).

GLEICHENIACEAE

Gleichenia Brackenridgei Fournier in Ann. Sci. Nat. sér. 5, xviii. 269 (1873).

Aneityum: Anelgauhat Bay, common in rain-forest at 750 m., no. 873, March 5, 1929 (large fern up to 1.8 m. high; a much smaller form is common on the waste-lands).

Gleichenia linearis (Burm.) Clarke in Trans. Linn. Soc. ser. 2, i. (Bot.) 428 (1880).

Tanna: Mt. Tokosh Meru, common in rain-forest at 800 m., no. 161, March 15, 1928.

Gleichenia oceanica Kuhn, Verh. Zool.-Bot. Ges. Wien, xix. 583 (1869).

Tanna: Mt. Tokosh Meru, common in rain-forest at 800 m., no. 160, March 15, 1928.

SCHIZAEACEAE

Schizaea dichotoma (L.) Smith in Mem. Acad. Sci. Turin, v. 422, t. 9, fig. 9 (1793).

Aneityum: Anelgauhat Bay, common in rain-forest at 150 m., no. 918, March 17, 1929 (small plant up to 0.60 m. high). *Eromanga*: Dillon Bay, common in rain-forest at 300 m., no. 286, May 23, 1928 (plant with single stem 40 cm.); common in poor red soil, bracken country at 400 m., no. 355, June 1, 1928 (small plant 20 cm. high).—Vernacular name "Nempari" (under no. 286).

According to the collector's note under no. 286 this plant has a remarkable history; if worn when a war was on in old heathen

days it was a sign that the wearer was a non-combatant and was respected as such; the name "Nempari" means peace-maker.

Lygodium reticulatum Schkuhr, Kryptog. Gew. i. 139, t. 139 (1809).

Aneityum: Anelgauhat Bay, common in rain-forest at sea level, no. 882, March 7, 1929 (climbing as high as 9 m. into trees). *Eromanga*: Dillon Bay, common in poor red soil, bracken country, at 300 m., no. 303, May 24, 1928 (climbing fern with a twining stem often 3-4 m. long; used by natives as a twine for house-building).—Vernacular name "Nor-rep" (under no. 303).

OSMUNDACEAE

Leptopteris Wilkesiana (Brack.) Christ, Farnkr. d. Erde, 334 (1897).

Aneityum: Anelgauhat Bay, common in rain-forest at 750 m., no. 869, March 5, 1929 (small tree fern up to 1.8 m. high; fronds up to 1 m. long).

OPHIOGLOSSACEAE

Ophioglossum pendulum Linnaeus, Sp. Pl. ed. 2, II. 1518 (1763).

Aneityum: Anelgauhat Bay, common in rain-forest at 210 m., no. 825, Feb. 28, 1929 (parasitic fern hanging down from a large *Asplenium*). *Tanna*: Lenakel, not common in rain-forest at 100 m., no. 139, March 8, 1928 (parasite on a large Banyan Fig).

LYCOPODIACEAE

Lycopodium cernuum Linnaeus, Spec. Pl. 1103 (1753).

Aneityum: Anelgauhat Bay, common in shade of rain-forest at 150 m., no. 854, March 4, 1929 (climbing Lycopod). *Tanna*: Mt. Tokosh Meru, common on shaded banks in rain-forest at 900 m., no. 158, March 15, 1928. *Efate*: Undine Bay, common in shade of bracken on high open hills at 250 m., no. 224, April 27, 1928.

Lycopodium oceanianum Herter in Bot. Jahrb. XLIII. beibl. 98, p. 52 (1909).

Efate: Undine Bay, Mt. McDonald, common in rain-forest at 600 m., no. 239, April 29, 1928 (parasite on trees).—Vernacular name "Tassel Fern."

Lycopodium Phlegmaria Linnaeus, Sp. Pl. 1101 (1753).

Aneityum: Anelgauhat Bay, common in rain-forest at 210 m., no. 824, Feb. 28, 1929 (growing upon trees).

Lycopodium squarrosum Forster, Fl. Ins. Austr. Prodr. 86 (1786).

Aneityum: Anelgauhat Bay, common in rain-forest at 300 m., no. 843, March 2, 1929 (spore cases light yellow before they burst, easily discernible at end of stem).

PSILOTACEAE

Psilotum complanatum Swartz, Syn. Fil. 188, 414 (1806).

Aneityum: Anelgauhat Bay, common in rain-forest at 150 m., no. 919, March 17, 1929 (parasite, up to 1 m. high; growing from holes and in forks of trees; sporangia cream-white, minute). *Eromanga*: Dillon Bay, common in rain-forest at 200 m., no. 377, June 7, 1928 (parasite hanging down from trees).—Vernacular name "Ami-ghokul" (under no. 377).

Psilotum nudum (L.) Grisebach in Abh. Ges. Wiss. Göttingen, VII. 278 (1857).

Tanna: Lenakel, rare in rain-forest at 150 m., no. 134, March 8, 1928 (parasite growing in crevices of roots of Banyan trees).

ADDITIONS

Vol. XII. 230

Heritiera litoralis Dryand.—Add: Already found on Efate.

Vol. XII. 260. Add under SAMYDACEAE:

Casearia Melistaurum Sprengel, Syst. II. 354 (1825).

Aneityum: Anelgauhat Bay, common in rain-forests up to 500 m., no. 981 (coll. J. P. Wilson), Sept. 1929 (small tree, trunk about 45 cm. diam.; flowers green, fruit clusters at base of leaves).—Also New Caledonia.—Vernacular name "Nidu-pualau."

Vol. XIII. 23. Add before *CORDIA MYXA*:

Cordia subcordata Lamarck, Tabl. Encycl. Méth. I. 421, n. 1899 (1791).

Efate: Fila Island, Vila, common on sea coast, no. 184, April 13, 1928 (tree about 8 m. high; natives say the fruit is eaten).—Already found on Efate; also New Caledonia, Loyalty Islands, Australia (Queensland), Society and Marquesas Islands, New Guinea and Malaysia.

MUSÉUM NATIONAL D'HISTOIRE NATURELLE,
PARIS.

CONTRIBUTION TO THE FLORA OF THE NEW
HEBRIDES AND SANTA CRUZ ISLANDS

ORCHIDS COLLECTED BY S. F. KAJEWSKI IN 1928 AND 1929

OAKES AMES

A. GUILLAUMIN, in his enumeration of the species that comprise the flora of the New Hebrides, included less than forty representatives of the Orchidaceae. With the exception of *Corymborchis*, *Bulbophyllum*, and *Habenaria* which is represented in the tropics of both hemispheres and, if broadly interpreted, extends into the temperate zones, all of the genera enumerated by Guillaumin are paleotropical.

Collections recently made by S. F. Kajewski in 1928 and 1929 for the Arnold Arboretum have increased substantially the orchid flora of the New Hebrides and the adjacent islands of the Santa Cruz Group. Several of the genera found by Kajewski are additions to the region and ten of the species are new. Unfortunately some of Kajewski's material was collected without flowers and admits only of tentative or suggestive identification.

Two courses are open to the student of a flora which is but little known and which shows a close relationship to the floras of distant regions: he may disregard slight differences between species in hand and species from other localities, and recast published descriptions so that they will include his material, or he may throw emphasis on slight differences and, in anticipation of more intensive exploration and a wider knowledge of the flora, interpret specific characters in a very narrow sense. In the following treatment I have adopted the latter course, being prompted to do so by the conviction that an erroneous extension of range for a genus or species is more detrimental to scientific progress than the increase of synonyms.

Corymborchis veratrifolia (Reinw.) Blume, Fl. Jav. nov. ser. i. 105, t. 43, fig. 1 (1858).

T a n n a: Mt. Tokosh Meru, terrestrial, in rain-forest at 200 m., no. 146, March 14, 1928 (pretty, white-flowered ground orchid, 1 m. high; sweetly scented).—Already found on Espiritu Santo (Campbell).

The flowers are somewhat smaller than in typical material. A still smaller flowered plant with narrower leaves, collected by Dr. R. Morrison on Efate, August 20, 1896, appears to belong here. (Herb. Kew.). It is probable that the specimens examined rep-

resent a new species, but until more material is available it would be unwise to separate Kajewski's specimens from *C. veratrifolia*. *C. veratrifolia* has already been reported as a native of the New Hebrides. It is a widely distributed species ranging from India to New Guinea.

***Malaxis neo-ebudica* Ames, sp. nov.**

Herba terrestris. Caules elongati, foliosi. Folia ovato-lanceolata, acuminata, in petiolum sulcatum contracta. Pedunculus elongatus. Bracteae inflorescentiae anguste lineares. Racemus cylindraceus, elongatus, multiflorus, floribus flavidis. Pedicellus cum ovario quam bractea subtendens paulo brevior. Sepala lateralia elliptica, uninervia, obtusa, in sicco pellucida. Sepalum dorsale anguste ellipticum, valde obtusum, uninervium. Petala lineari-oblonga, obtusa, uninervia. Labellum trilobatum, lobi laterales post columnam in auriculas elongatas producti, lobus medius plus minusve triangulus, haud retusus, utrinque paucidentatus.

Stem up to 12 cm. long, ascending, bearing about 10 membranaceous leaves. Leaves variable, the lowermost ones much the smallest, uppermost leaves about 13 cm. long, up to 3 cm. wide, contracted at base into broad sheathing petioles, lanceolate, acuminate-acute. Peduncle slender, conspicuously angulate when dry, together with the raceme about 14 cm. long. Raceme slender, about 10 cm. long, many-flowered. Bracts of the inflorescence elongated, linear-lanceolate, about 7 mm. long, exceeding the flowers. Pedicellate ovary about 5 mm. long. Flowers yellow. Lateral sepals 2 mm. long, about 1 mm. wide, elliptical, obtuse, 1-nerved, spreading. Upper sepal similar, but slightly narrower. Petals about 2 mm. long, linear-oblong, obtuse, 1-nerved. Labelum 3-lobed, including the lateral lobes 3.5 mm. long. Lateral lobes auriculate, about 2 mm. long, narrowly triangular, acute or obtuse, twice or thrice longer than the column. Middle lobe 1.5 mm. long from tip to point of attachment, triangular, terminating in a bluntly triangular lobule on either side of which there are 2-3 irregular teeth.

Tanna: Lenakel, small plant growing in shade of large trees; flowers yellow; alt. 100 m. in rain-forest. No. 137 (type in Herb. Ames no. 36366), March 8, 1928.

The nearest ally of this species appears to be *M. bancana* (Ridl.) O. Ktze. from which it differs in the structure of the lip. *M. oculata* (Reichb. f.) O. Ktze. is also a closely allied species, but differs vegetatively from *M. neo-ebudica*.

***Malaxis xanthochila* (Schltr.) Ames & Schweinfurth in Ames, Orch. vi. 73 (1920).**

Microstylis xanthochila Schlechter in K. Schumann & Lauterbach, Nachtr. Fl. Deutsch. Schutzgeb. 102 (1905).

A n e i t y u m: Anelgauhat Bay, common in rain-forest at sea level, no. 837, March 1, 1929 (small plant up to 1 ft. high; flowers yellow). —Also New Guinea.

Two specimens which are referable to this species, one collected by Dr. R. Morrison on Aneityum at Anelgauhat in June 1896, the other collected by L. Cheeseman at South West Bay, Malekula in January 1930, are preserved in the Kew Herbarium. Although the basal auricles of the lip in the Malekula plant are longer than is typical, it agrees in essential characters with *M. xanthochila*. **Malaxis lunata** (Schltr.), comb. nov. (*Microstylis lunata* Schlechter in Fedde Rep. Spec. Nov. IX, 162 [1911]) differs from *M. xanthochila* in the basal auricles of the labellum and in the spatulate petals. The type specimen of *M. lunata* was collected by Dr. Morrison on Aneityum near Anelgauhat.

Liparis condylobulbon Reichenbach f. in Hamb. Gartenz, XVIII: 34 (1862).

Liparis confusa J. J. Smith, Fl. Buitenz. VI. (Orch. Jav.) 275 (1905).

E r o m a n g a: Dillon Bay, common in rain-forest at 400 m., no. 321, May 29, 1928 (growing on trees thickly shaded from the sun). **B a n k s G r o u p**: Vanua Lava, common in rain-forest at 350 m., no. 455, July 10, 1928 (orchid growing in dense shade on small tree in gully; perianth organs small, outer ones pale green, inner ones brown).—Vernacular name "Ute-melme-pohl" (under no. 321).

In the Kew Herbarium there are five specimens representing this species, obtained in Aneityum in 1896 by Dr. R. Morrison. This is one of the most widely distributed species of the genus, being very common in the Philippines, Sumatra, Java, Celebes, Borneo and New Guinea.

Coelogyne asperata Lindley in Jour. Hort. Soc. IV. 221 (1849).

S a n t a C r u z G r o u p: Vanikoro, common in rain-forest at sea level, no. 679, December 4, 1928 (beautiful, large-leaved orchid common on trees in Vanikoro; leaves dark green; flower yellow-cream, orange center; most beautiful of Vanikoro orchids).

The specimen collected was in bud, and not wholly satisfactory for identification, but there is sufficient evidence to warrant referring it to the widespread *C. asperata*, a species which ranges from the Malay Peninsula to Sumatra, Borneo, the Philippine Islands and New Guinea.

Coelogyne lamellata Rolfe in Kew Bull. 1895, 36.

S a n t a C r u z G r o u p: Vanikoro, common in rain-forest at sea level, no. 687, December 5, 1928 (large-leaved orchid common in the scrub on large trees; flower light yellow-green).

Pholidota imbricata Lindley in Hook. Exot. Fl. II. t. 138 (1825).

Santa Cruz Group: Vanikoro, common in rain-forest at sea level, no. 681, December 4, 1928 (orchid common on trees close to salt water creek; fruit yellow, brown when ripe). **Eromanga:** Dillon Bay, common orchid on trees in gullies in rain-forest at 300 m., no. 390, June 8, 1928 (capsules opened when ripe and the seeds put on the natives' faces as a substitute for the face powder of commerce).

The material, on which the identification of no. 681 rests, is devoid of flowers. It is highly probable that this material is conspecific with *P. grandis* Kraenzl. apud Guillaumin in Bull. Soc. Bot. France, LXXVI. 301 (1929), non Ridl. in Jour. Str. Br. Roy. Asiat. Soc. XLIX. 32 (1907). Kraenzlin described *P. grandis* with the aid of fruiting specimens to which only vestiges of the flowers adhered. In view of the occurrence of what appears to be *P. imbricata* on Eromanga, and taking into consideration the extensive range of this species, from India to Burma, Assam, Siam, Malay Peninsula, China, Sumatra, Java, the Philippine Islands, Celebes, Borneo and New Guinea, I suspect that *P. grandis* Kraenzl. is referable to it.— Vernacular name "Utnimpoll" (under no. 390).

Pseuderia vanikorensis Ames, sp. nov.

Caules elongati, vaginis foliorum omnino obtecti, plus minusve flexuosi. Folia disticha, anguste lanceolata, usque ad apicem attenuata, acuta. Vaginae foliorum tubulatae, arcte adpressae. Racemi pauciflori, laterales. Sepala lateralia falcata, valde carinosa, leviter carinata. Sepalum dorsale spathulatum, concaviusculum, plus minusve rigidum, prope apicem carinatum. Petala oblongo-ligulata, apicem versus paulo latiora, obtusa, uninervia. Labellum ellipticum, subacutum, dense papillosum; callus linearis in disco decurrens. Columna carinosa, arcuata, in pedem brevem producta, labello articulata.

Stems 5–6 dm. long, slender, about 6 mm. in diameter, concealed by the sheathing bases of the leaves, more or less flexuose. Leaves numerous, distichous, 13–14 cm. long, about 2.5 cm. wide, 2–2.5 cm. apart, narrowly lanceolate, tapering gradually to an acute tip, rounded at the base and contracted into a short sulcate petiole. Petiole articulate with a tubular sheath. Racemes produced on the upper part of the stem, distichous, 2.5–3 cm. long. Bracts of the raceme lanceolate, rigid, shorter than the pedicels, blackish when dry. Pedicel with the ovary about 8 mm. long, glabrous, slender. Lateral sepals shorter than the dorsal sepal, 8 mm. long, about 2.5–3 mm. wide above the middle, very fleshy, rigid, falcate-oblong, obtuse, deflexed, carinate along the middle nerve on the outer surface.

Dorsal sepal 1 cm. long, 2 mm. wide above the middle, concave-spatulate, obtuse, conspicuously carinate near the tip on the outer surface, arcuate. Petals about 7.5 mm. long, 1.5 mm. wide, oblong-ligulate, obtuse, slightly broader near the tip than at the base, 1-nerved, slightly curved, fleshy. Labellum about 5 mm. long, hardly 4 mm. broad at the middle, elliptic, subacute, densely papillose, margin ciliate. Disc with a fleshy keel extending from the base of the labellum almost to the apex on the inner surface; keel sulcate at the base. Column 5 mm. long, arcuate, produced at base into a short foot with which the labellum is articulated.

Santa Cruz Group: Vanikoro, in rain-forest at 150 m., no. 669 (type in Herb. Ames, no. 37190), December 3, 1928 (large climbing orchid hanging from rain-forest trees; leaves light green and glossy; flowers purple splashed with yellow).

In general facies this species closely resembles *Pseuderia frutex* Schltr. but differs in the form of the labellum.

Dendrobium (§ Aporum) sp.

E f a t e: Fila Island, Vila, common on rocky beach, no. 190, April 14, 1928 (small orchid growing on large rocks close to salt water).

The specimens are in fruit and indeterminable. Vegetatively the plants resemble closely *Dendrobium ventricosum* Kraenzl. from the Philippines.

Dendrobium Goldfinchii F. v. Mueller in Wing's South. Sci. Rec. (Jan. 1883).

Santa Cruz Group: Vanikoro, common at sea level, no. 636, November 20, 1928 (growing on rain-forest trees).—Already found on Aurora (*Im Thurn*, no. 341).—Also New Guinea and Admiralty Islands.

Dendrobium Kajewskii Ames, sp. nov.

Caules elongati, foliosi. Folia coriacea, elliptica vel elliptico-oblonga, apice inaequaliter bilobata. Pedunculi validi, elongati. Racemi multiflori. Sepala lateraliter anguste triangularia, undulata, mentum formantia. Sepalum dorsale simile. Petala ligulata. Labellum trilobatum; lobi laterales rotundati, verrucosi; lobus medius ovatus; discus tricarinatus. Columna sectionis.

Roots elongated, about 2 mm. in diameter, whitish. Stems about 2.5 dm. or more tall, jointed, the upper internodes swollen; nodes 3–3.5 cm. apart. Leaves coriaceous, 5–11 cm. long, 2.5–3 cm. wide, elliptic to elliptic-oblong, unequally bilobed at the apex, contracted at base into closely appressed complanate sheaths,

only the uppermost leaves persisting at anthesis. Peduncles including the raceme elongated, up to 4 dm. long, 3 mm. or more in diameter, rigid, obliquely ascending, produced opposite the leaves, paucibracteate below the racemes. Bracts tubular, closely appressed, scarious. Racemes many-flowered, about 2 dm. long. Bracts of the raceme scale-like, much shorter than the pedicels. Pedicels slender, ascending, with the ovary 2.5 cm. long. Flowers large and showy. Lateral sepals 2.2 cm. long, about 5 mm. wide, narrowly triangular, undulate margined, acute, forming with the elongated foot of the column a subacute mentum. Upper sepal about 2 cm. long, 7 mm. wide, oblong-lanceolate, acute, 5-nerved, undulate margined. Petals ligulate, about 2.8 cm. long, 4 mm. wide, undulate margined. Labellum 2.5 cm. long, about 1.5 cm. wide, 3-lobed; lateral lobes rounded in front, rugulose or verrucose on the inner surface, about 1.5 cm. long; midlobe hardly 1 cm. long, 6 mm. wide, ovate, acute, undulate margined. Disc provided with three thickened keels. Column including the foot 1.5 cm. long, free portion 5 mm. long.

Santa Cruz Group: Vanikoro, common in rain forest, no. 638a (type in Herb. Ames, no. 37111) and 638b, November 20, 1928 (common orchid in the scrub on mangroves).

Under no. 638, Kajewski collected a series of specimens which differed from one another in floral characters and appeared to be separable. To these specimens he assigned the numbers 638, 638a and 638b. Number 638 is referable to *Dendrobium macranthum* A. Rich. Numbers 638a and 638b are conspecific differing from one another only in the color of the flowers and in slight differences in the form of the midlobe of the labellum. In 638a the prevailing color is yellow with purple lines, the labellum being greenish-yellow with purple striations. In 638b the sepals and petals are dull purple on the inner surface with bright yellow margins, while the labellum is bright yellow-green with purple lines and dots.

Dendrobium Kajewskii differs from *D. macranthum* in the undulate sepals and the very different labellum. From the closely allied *D. conanthum* Schltr., it differs chiefly in lacking supplementary carinae on the disc of the labellum and in having the lateral lobes verrucose or rugulose on the inner surface.

Dendrobium macranthum A. Richard, Sert. Astrol. 15, t. 6 (1832).

Santa Cruz Group: Vanikoro, common in rain-forest, no. 638, November 20, 1928 (common orchid both in the scrub and on mangroves). This species was originally found on Vanikoro Island.—Also Samoa. The flowers are somewhat smaller than in typical *D. macranthum*.

Dendrobium (§ *Dendrocoryne*) *macrophyllum* A. Richard, Sert. Astrol. 22, t. 9 (1834).

Santa Cruz Group: Vanikoro, common in rain-forest at sea level, no. 637, November 20, 1928 (a common orchid; flower yellow with purple spots, very pretty).—Also New Guinea, Java and the Philippine Islands.

Dendrobium separatum Ames, sp. nov.

Caules elongati, validi, foliosi. Folia disticha, oblongo-lanceolata, apice inaequaliter bilobata, acuta, in sicco chartacea. Racemi laterales, plus minusve decemflori. Flores congesti, aurantiaci. Sepala lateralia oblonga, subacuta, mentum elongatum formantia. Sepalum dorsale oblongum, prope apicem angustatum, subacutum vel obtusum. Petala margine minute erosa, elliptico-lanceolata, obtusa vel subacuta, concaviuscula, uninervia. Labellum elongatum, simplex, infra medium leviter constrictum, superne in laminam oblongo-ellipticam productum, lamella transversa ornatum; lamella denticulata. Columna generis.

Stems up to 1 m. long, stout, leafy, concealed by the sheathing bases of the leaves, yellow after the fall of the leaves, deeply sulcate in dried specimens. Leaves spreading, 1.5–2 dm. long, 1.9–2.5 cm. wide, oblong-lanceolate, tapering to an acute unequally bilobed tip; internodes about 2.5 cm. long. Peduncles lateral on defoliated stems, including the raceme about 2 cm. long, produced at the nodes, rather fleshy, ascending or at right angles with the stem. Racemes about 1.5 cm. long, about 2 cm. in diameter, bearing ten or more orange flowers. Bracts of the raceme about 3 mm. long, narrowly lanceolate, acute, rigid. Flowers 1.5 cm. long, fleshy. Lateral sepals 1.4 cm. long including the mentum, 2.5 mm. wide, oblong, subacute, strongly concave, fleshy. Upper sepal 5 mm. long, oblong, narrowed to a rounded or subacute apex, strongly concave. Mentum about 9.5 mm. long, forming a blunt spur which is open in front. Petals 5 mm. long, about 2 mm. wide, elliptic-lanceolate, obtuse, with an erose margin, 1-nerved. Labelum 1.3 cm. long, slightly constricted below the middle, simple, 3 mm. wide above the middle, dilated upward forming an oblong-elliptic smooth lamina with the apical margin slightly inrolled, traversed, where it is constricted, by a fleshy retrorse plate which is minutely denticulate. Column including the foot 11 mm. long, fleshy.

Santa Cruz Group: Vanikoro, in rain-forest on giant Kauri at 350 m., no. 503 (type in Herb. Ames 37154), September 9, 1928 (straggling orchid up to 1 m. long, hanging in strings; flowers orange; found only on old stems).

This species has the general facies of *Dendrobium triviale* Kraenzl. but differs in the structure of the labellum and in having the transverse plate or lamella on the disc distinctly erose on the upper edge. The transverse lamella which serves as a dividing wall between the basal and apical parts of the labellum suggests the specific name of the plant.

***Dendrobium vanikorense* Ames, sp. nov.**

Planta *D. acuminatissimo* habitu omnino congruens. Caules pergraciles, elongati. Folia disticha, linearia, acuta. Flores singuli, e nodis superioribus exorientes. Sepala lateralalia anguste triangularia, acuta, mentum obtusum formantia. Petala linearia, usque ad apicem attenuata. Labellum anguste ellipticum, margine denticulato vel breviter fimbriato; callus angustus prope basim stat. Columna generis.

Stems up to 1 m. long, about 1.5 mm. in diameter, yellowish, concealed by the tubular sheaths with which the leaves are articulated. Leaves distichous, 8–11 cm. long, about 3 mm. wide, tapering gradually to an acute tip, linear-triangular, about 12 mm. apart. Inflorescence breaking through the leaf-sheaths opposite the leaves, 1-flowered, alternating on the upper part of the stem. Peduncle 6 mm. long, subtended by a closely appressed complanate bract about 5 mm. long. Lateral sepals 12–15 mm. long, about 3 mm. wide above the mentum, narrowly triangular, acute, forming an obtuse mentum 4 mm. long. Upper sepal 14–16 mm. long, similar to the laterals, subcaudate at the tip. Petals 12–15 mm. long, about 1 mm. wide near the base, linear, tapering gradually to the acute caudate tip, 3-nerved. Labellum simple, 11 mm. long, 4–5 mm. wide, elliptical with a shortly fringed or denticulate margin, upper surface thickly studded with simple or several-toothed, complanate processes, and provided near the base with an elongated central callus 4 mm. long. Column fleshy, stout, including the foot 6 mm. long.

Santa Cruz Group: Vanikoro, common in rain-forest at 50 m., no. 663 (type in Herb. Ames, no. 37191), November 28, 1928 (orchid up to 1 m. long, hanging down from the rain-forest trees; flower creamy yellow tinged with purple); poor red soil in rain-forest at 50 m., no. 657, November 25, 1928 (a common orchid growing on small trees; flowers whitish); a sterile specimen which is vegetatively similar to no. 663.

In general habit this species resembles *D. acuminatissimum* Lindl. from which it differs chiefly in having a simple lip. *D. indragiriense* Schltr. and *D. holochilum* Schltr. are closely allied species but differ both vegetatively and florally from *D. vanikorense*.

***Eria Kajewskii* Ames, sp. nov.**

Radices fibratae, pubescentes. Pseudobulbi cauliformes, clavati, bracteis vaginantibus omnino obtecti. Folia prope apicem pseudobulbi conferta, oblonga, utrinque attenuata, apice inaequaliter bilobata. Pedunculi e parte superiore pseudobulbi exorientes, foliis multo breviores, glabri. Bracteae inflorescentiae in sicco brunneae, ellipticae. Pedicellus cum ovario gracilis, elongatus. Sepala lateralibus anguste triangularia, acuta, mentum formantia. Sepalum dorsale simile. Petala oblongo-lanceolata, acuta. Labellum ovatum, margine irregulariter dentatum; discus glaber, prope basim bicallosus. Columna generis.

Roots fibrous, elongated, branching, finely pubescent. Pseudobulbs stemlike, 14–17 cm long, clavate, when dry 7 mm. in diameter near the base, up to 11 mm. in diameter near the summit, concealed by brownish tubular closely appressed sheaths, the upper portion bearing about 5 more or less crowded leaves. Leaves 11.5–17 cm. long, 1.5–2 cm. wide, oblong, narrowed toward the ends, unequally bilobed at the apex. Peduncles arising from the upper part of the pseudobulb, interspersed among the leaves, about 9 cm. long, floriferous almost to the base. Flowers about 15 in a loose raceme. Floral bracts elliptic, brownish when dry, about 5 mm. long. Pedicel with the ovary about 1 cm. long, slender. Lateral sepals 11 mm. long, about 3 mm. wide at the base, narrowly triangular, acute, forming with the foot of the column a short obtuse mentum, 3-nerved; mentum 2 mm. long. Upper sepal 11 mm. long, about 2 mm. wide, oblong, acute, 3-nerved. Petals 9–10 mm. long, 2.5 mm. wide near the base, oblong-lanceolate, acute, 3-nerved, the outer nerves branched. Labellum 5 mm. long, about 2.5 mm. wide, rather fleshy, smooth, ovate, acute or subacute, margin with several blunt teeth on either side above the middle, 3-nerved with the outer nerves branching, bicallose near the base; calli abbreviated, one on each outer nerve. Column including the foot 5 mm. long.

An e i t y u m : Anelgauhat Bay, common in rain-forest at 200 m., no. 820 (type in Herb. Ames, no. 37850) (small orchid growing on trees; flowers inconspicuous).

Eria Kajewskii is closely allied to *E. retroflexa* Lindl. which it resembles closely in habit, but it is clearly distinguishable from that species and from all close allies in having the margin of the labellum bluntly dentate above the middle.

***Eria vanikorensis* Ames, sp. nov.**

Caules elongati, erecti, vaginis foliorum omnino obtecti. Folia disticha, oblonga, utrinque attenuata, quam racemus longiora,

dense fusco-villosa, in petiolum vaginantem contracta. Racemi pauciflori, rubro-villosi. Bracteae inflorescentiae dense rufo-villosae, anguste ovatae, rigidae. Flores tomento rufo vestiti. Sepala lateralia triangulari-lanceolata, valde incrassata, intus et extus dense rufo-villosa, mentum obtusum formantia. Sepalum dorsale triangulari-lanceolatum. Petala oblonga, obtusa, extus dense rufo-villosa, leviter concava. Labellum prope apicem conspicue constrictum lobum transverse ellipticum vel reniformem formans, per lobum medium callo prominenti ornatum, inferne usque ad basim attenuatum; discus intus villosus, per medium 4-nervius. Columna generis.

Stems up to 1 m. long, concealed by the cylindrical foliar sheaths with which the leaves are articulated; sheaths 1.5–3 cm. long, densely covered with brownish, more or less matted hairs. Leaves distichous, up to 12.5 cm. long, 1.7–2.5 cm. wide, oblong-lanceolate, coriaceous, densely pubescent above, covered beneath with reddish appressed hairs. Racemes 5 or more, produced on the upper part of the stem, situated opposite the leaves, about 3.5 cm. long with a cupuliform sheath at the base. Rachis of the raceme densely reddish villose. Bracts subtending the pedicels about 1 cm. long, rigid, covered with reddish hairs. Ovary sessile, up to 2 cm. long, covered with reddish hairs. Flowers about 1 cm. long. Lateral sepals 1 cm. long, about 5 mm. wide near the base, triangular-lanceolate, acute, covered inside and out with bristle-like reddish hairs, fleshy, rigid, forming a prominent obtuse mentum. Upper sepal about 1 cm. long, similar to but narrower than the laterals. Petals 8 mm. long, 1.5 mm. wide, linear-oblong, rounded at the tip, sparsely pubescent inside, conspicuously hairy on the outside, mid nerve prominent. Labellum about 1 cm. long, 3 mm. wide, constricted 2 mm. below the apex forming a terminal reniform or transversely elliptical lobe; lamina oblong, contracted toward the base, ornamented inside and out with long closely appressed or slightly spreading reddish hairs; disc 4-nerved, ecarinate, with a short fleshy callus extending along the middle of the terminal lobe. Column characteristic of the genus.

Santa Cruz Group: Vanikoro, common in rain-forest, alt. 50 m., no. 512 (type in Herb. Ames no. 37110), September 20, 1928.

Allied to *E. iodantha* Schltr. from which it differs in the structure of the lip.

Mediocalcar vanikorense Ames, sp. nov.

Herba epiphytica. Radices dense pubescentes. Rhizoma validum, elongatum, arcte vaginatum, vaginis brunneis obtectum.

Pseudobulbi obpyriformes, in sicco valde sulcati, monophylli, statu juvenili vaginis vestiti. Folium variabile, 3.5–7.5 cm. longum, 1–1.7 cm. latum, valde coriaceum, oblongum vel oblanceolato-oblongum, apice tridentatum. Pedunculi uniflori ut videtur, singuli vel bini, folium aequantes vel breviores, plus minusve 4 cm. longi, paucibracteati, bracteis acuminatis. Flos 1 cm. longus, aurantiacus. Sepala cupulam formantia, ovata usque ad medium cohaerentia. Petala lineari-lanceolata, trinervia. Labellum prope medium valde calcarato-saccatum, ovato-acuminatum. Columna valida, labello brevior.

Rhizome rather stout, elongated, when young concealed by brownish tubular bracts, those subtending the pseudobulbs broadly ovate, chartaceous. Roots fibrous, elongated, branching, densely pubescent. Pseudobulbs 1–1.5 cm. long, obpyriform, longitudinally sulcate, monophyllous. Leaf extraordinarily variable, coriaceous, 3.7–7.5 cm. long, 1–1.7 cm. wide, oblong or oblong-oblanceolate, tapering gradually to a blunt bilobed apex, the midnerve extended into an apicule that almost equals the lobes in length. Peduncles single or geminate, shorter than or equalling the leaf, including the pedicellate ovary 2.5–4 cm. long, one-flowered, slender, only one peduncle floriferous at a time. Pedicel and ovary 1–1.5 cm. long, subtended by a scale-like acuminate bract. Flower urceolate, 1 cm. long, orange with the tip of the sepals yellow. Sepals similar, ovate-lanceolate, about 4 mm. wide at the point of union, free portion about 4 mm. long, united for more than half their length, the lateral ones forming a protuberant blunt mentum. Petals free, about 9.5 mm. long, hardly 2 mm. wide, linear-lanceolate, acute, 3-nerved. Labellum about 9 mm. long, parallel with the column, erect, with a rounded blunt sac near the middle; lamina ovate, acuminate-acute from a broad base. Column 6 mm. long.

Santa Cruz Group: Vanikoro Island, common on large trees at 50 m., no. 641 (type in Herb. Ames no. 37194), November 22, 1928. Also from the New Hebrides, Eromanga, Peak south of Dillon Bay, Dr. R. Morrison, August 5, 1896 (Herb. Kew). N. E. Traitor's Head, summit of old crater growing on rotten trunk, 2,400 feet alt., L. Cheeseman, no. 71 (Herb. Kew). Aneityum, Peak of Ithumu, Dr. Morrison, June 30, 1896 (Herb. Kew).

The genus *Mediocalcar* has not been reported heretofore from the New Hebrides or from the Santa Cruz Group. *M. vanikorensis* is an ally of *M. bulbophylloides* J. J. Sm. differing from it in the widely separated pseudobulbs, larger leaves and in the color of the flowers. *Mediocalcar* is essentially New Guinean with very few outlying species. *M. ponapense* Schltr., from the Caroline

Islands, one of the few species reported from beyond New Guinea, differs from *M. vanikorense* in being much more robust, with larger pseudobulbs and dissimilar leaves.

Ceratostylis kaniensis Schlechter in Fedde Rep. Spec. Nov. Beihefte 1. 245 (1912).

Santa Cruz Group: Vanikoro, common in rain-forest at 150 m., no. 575, November 6, 1928 (a plant found on a large Kauri tree).—Also New Guinea.

Ceratostylis subulata Blume, Bijdr. 306 (1825).

E f a t e: Undine Bay, common in rain-forest at 500 m., no. 234, April 28, 1928 (growing on bark of tree).—Also Java, Sumatra, Malay Peninsula, Assam.

The material studied lacks flowers and leaves. In general aspect the plant resembles *C. kaniensis* Schltr.

Earina Brousmichei Kraenzlin in Lecomte, Notulæ Syst. iv. 136 (1928).

A n e i t y u m: Anelgauhat Bay, common in rain-forest at 1000 feet, no. 844, March 2, 1929 (orchid growing on rain-forest trees; flowers white).—Also New Caledonia.

Kajewski's specimen differs from the type in being taller with much longer leaves. A flowerless plant from Efate, Undine Bay collected by Dr. Morrison in August 1896 appears to belong here (Herb. Kew).

Appendicula reflexa Blume, Bijdr. 301 (1825).

A n e i t y u m: Anelgauhat Bay, common in poor red soil country at 500 feet, no. 915, March 17, 1929 (ground orchid 2 ft. high; flower white and green). **E r o m a n g a:** Dillon Bay, common in poor red soil, bracken country, no. 326, May 29, 1928 (orchid growing on ground in shade of bracken and stunted brush; flower white).—Also Sumatra, Borneo, Celebes, and the Malay Peninsula.—Vernacular name "Orvum-nge-nompull" (under 326).

Appendicula vanikorensis Ames, sp. nov.

Herba gracilis. Caules vaginis foliorum omnino obtecti. Folia disticha, lanceolato-lineariter, acuminata, apice rotundato-bilobulata, basi amplexantia. Inflorescentiae omnino laterales. Sepala lateraliter late triangulariter, trinervia, mentum obtusum formantia. Sepalum dorsale anguste ellipticum. Petala oblongo-lanceolata, valde obtusa, uninervia. Labellum simplex, carina hippocrepi-formis instructum.

Stems slender, 1.5 dm. long in the fragments that were collected, probably attaining a height of 25 or 30 cm., entirely concealed by the

sheathing tubular bases of the leaves, flexuose. Leaves distichous, 3.5–5.5 cm. long, 8–15 mm. wide, about 1 cm. apart, narrowly lanceolate, bluntly bilobed at the tip with the midnerve projecting between the lobes, obliquely ascending. Inflorescences opposite the leaves, breaking through the tubular sheaths with which the leaves are articulated, about 1 cm. long, several-flowered. Bracts of the inflorescence about 3 mm. long, rigid, lanceolate. Lateral sepals about 3 mm. long including the blunt mentum, about 2 mm. wide at the base, strongly concave, broadly triangular, ending in a much thickened tip, 3-nerved. Upper sepal about 2.5 mm. long, approximately 1 mm. wide, narrowly elliptical, obtuse, 3-nerved, thickened at the apex, strongly concave. Petals 2 mm. long, 1 mm. wide, oblong-lanceolate, rounded at the apex, usually 1-nerved. Labellum 3 mm. long, 2 mm. wide, simple, lightly saccate at the broad base, in front of the sac expanded into a more or less elliptical obtuse lamina with an apical callus; sac with a large callus in the center; callus transversely elliptical with the ends continued into thickened keels. Column including the foot 2 mm. long, rostellum bifid.

Santa Cruz Group: Vanikoro, in rain-forest at 300 m., no. 594 (type in Herb. Ames, no. 37193), November 11, 1928 (orchid growing on rocks in a gully with water running around them; flowers greenish white).

In general aspect this plant resembles *A. anceps* Bl. but is dissimilar from it in the structure of the lip. *A. reflexa* Bl. is also a close ally but different from *A. vanikorensis* chiefly in the shape of the petals.

Calanthe Vaupeliana Kraenzlin in Notizbl. Bot. Gart. Berlin, XLIV. 111 (1907).

Santa Cruz Group: Vanikoro, common in rain-forest at 800 m., no. 599, November 11, 1928 (a ground orchid a meter high, found growing at high altitudes; flower beautiful, white, length of flower stalk 70 cm.).—Also Samoa.

Three specimens from the New Hebrides, collected on Aneityum in June 1896 by Dr. Morrison, are preserved in the Kew Herbarium. One of these specimens from Anelgauhat is described as having had yellow flowers, another specimen from ranges above Anelgauhat collected on June 4, 1896 is said to have had white flowers. Structurally the plants collected by Kajewski on Vanikoro and by Morrison on Aneityum are similar and agree in essential characters with *C. Vaupeliana*. The apical lobe of the labellum is variable. In the type it is oblong; in Morrison's specimens it is strongly dilated from the base. Kajewski's specimen, with regard

to the lip, is almost intermediate between Vaupel's Samoan plants and Morrison's plants from Aneityum.

Spathoglottis Petri Reichenbach f. in Gard. Chron. n. ser. VIII. 392 (1877).

E r o m a n g a: Dillon Bay, common in red soil, bracken country at 300 m., no. 306, May 24, 1928 (ground orchid 1.5 m. high with pretty pale puce flowers).—Vernacular name "Lar-ver-ae."

In the Kew Herbarium there are three specimens from the New Hebrides, that are referable to *S. Petri*. Two of these were collected by Dr. R. Morrison on Aneityum near Anelgauhat in 1896. The third one was collected in March 1930 on Eromanga by L. Cheeseman (no. 14).

Spathoglottis Vieillardii Reichenbach f. in Linnaea, XLI. 85 (1877).

S a n t a C r u z G r o u p: Vanikoro, common in rain-forest at sea level, no. 563, November 6, 1928 (a ground orchid common throughout the New Hebrides; color of the flowers varies from white to purple; diameter 4 cm.; inside of flower yellow).—Already reported from Tanna.—Also New Caledonia.

Bulbophyllum sp.

S a n t a C r u z G r o u p: Vanikoro, common in rain forest at 150 m., no. 680, December 3, 1928 (an orchid growing on trees close to the sea; flowers dark red, inconspicuous petals; fruit 5 cm. long, 2.4 cm. in diameter).

This species is in advanced fruit. It is probably referable to *B. praealtum* Kraenzl. from Samoa, but the flowers are too old to be serviceable in attempts at identification. In general habit the plant resembles closely *Macrolepis longiscapa* A. Rich. and may be identical with it. *Macrolepis longiscapa* was originally found on Vanikoro. The genus *Macrolepis* is referable to *Bulbophyllum*, but Richard's species has never been transferred to *Bulbophyllum*. *B. longiscapum* Rolfe from Fiji would appear from the description to belong in the same alliance with Richard's species and with *B. praealtum* Kraenzl. Until a critical study of these species has been made it would be unwise to propose a new name under *Bulbophyllum* for Richard's *Macrolepis longiscapa*.

Vandopsis Warocqueana (Rolfe) Schlechter in K. Schumann & Lauterbach, Nachtr. Fl. Deutsch. Schutzgeb. 225 (1905).

S a n t a C r u z G r o u p: Vanikoro, common in rain-forest at 150 m., no. 586, November 8, 1928 (climbing orchid going up trees that are more or less leaning; flower yellowish green with light purple spots).—Also New Guinea.

Vandopsis Quaipei (Rolfe) Schltr. from Espiritu Santo is a closely allied species and may prove to be conspecific with *V. Warocqueana*. In the Kew Herbarium there is a specimen from Aneityum that is surely referable to *V. Warocqueana*, but it is in a fruiting condition and hardly satisfactory for critical study. This specimen was collected by Dr. R. Morrison on June 20, 1896 on the coast east of Anelgauhat.

***Saccolabium Kajewskii* Ames, sp. nov.**

Caules vaginis foliorum obtecti. Folia ligulata, coriacea, utrinque attenuata, apice inaequaliter et obtuse bilobulata, basi in petiolum brevem conduplicatum contracta. Pedunculus elongatus, infra racemum paucibracteatus, bracteis infundibuliformibus. Racemus cylindraceus vel cylindraceo-secundus. Sepala anguste ovata vel elliptica. Petala elliptica, acuta vel subobtusa, trinervia. Labellum longe calcaratum; lamina infra apicem suborbicularis, antice in apicem complanatum contracta.

Stem about 5 cm. or more long, rigid, completely concealed by the sheaths to which the leaves are articulated. Leaves distichous, 14–21 cm. long, up to 2 cm. wide, oblong, ligulate, unequally and bluntly bilobed at the apex. Peduncle with the raceme up to 19 cm. long, with about 3 infundibuliform bracts. Raceme up to 9 cm. long, densely many-flowered. Bracts of the inflorescence scale-like, very much shorter than the pedicels, 1.5 mm. long. Pedicel with the ovary 9 mm. long. Flowers including the spur of the lip 1.3 cm. long. Lateral sepals about 5 mm. long, 2 mm. wide, ovate or elliptical, obtuse, concave. Upper sepal similar. Petals about 5 mm. long, 2 mm. wide, elliptical, acute, 3-nerved. Labellum including the spur 1 cm. long, in front dilated into an orbicular lamina which terminates in a complanate tip; lamina with an intramarginal keel; spur 7 mm. long, inflated below the middle. Column 1.5 mm. long.

E f a t e: Undine Bay, common in rain-forest along sea shore, no. 205 (type in Herb. Ames no. 36375), April 4, 1928 (color of flowers ranging from creamy white to white with green, some purple, others pink). **B a n k s G r o u p:** Vanua Lava, common along sea shore, no. 448, July 9, 1928 (found growing close to the sea on trees whose trunks are well shaded).

Two specimens referable to this species are in the Kew Herbarium. They were collected on Efate, Undine Bay, in August 1896 by Dr. R. Morrison. One of these specimens differs from the type in having broader leaves.

ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

A NEW GENUS OF THE ORCHIDACEAE FROM THE NEW HEBRIDES

OAKES AMES

AMONG the orchids collected in the New Hebrides by Dr. R. Morrison in 1896 and by L. Cheeseman in 1930, there is a strikingly distinct species from Eromanga Island. I have been unable to refer it to any genus heretofore described. In general facies it suggests some of the species of the African genus *Acrolophia*, but is clearly differentiated by the very dissimilar means by which the pollen masses are attached to the viscid disc of the rostellum, by the absence of a well developed spur at the base of the labellum and by the aspect of the inflorescence.

For the opportunity of studying the material on which the following description is based I am indebted to the Director of the Royal Botanic Gardens, Kew.

Trichochilus Ames, gen. nov.

Divisio: *Acrotonae*; Tribus: *Kerosphaerinae*; Subtribus: *Polystachyeae*. Sepala lateralia patentia, basi columnae pedi affixa. Sepalum dorsale liberum. Petala sepalis similia. Labellum cum pede columnae inarticulatum, basi contracta incumbens, dein erectum, trilobatum, in saccum vel calcar abbreviatum plus minusve globosum productum, antice in laminam plus minusve pilosam productum, prope basim laminae bicallosum; lobi laterales patentes. Discus labelli conspicue papillosus vel pilosus. Columna elongata, in pedem brevem producta. Anthera terminalis, bicularis. Pollinia duo, globosa, stipitibus duobus distinctis affixa, glandula unica.—Herba terrestris. Folia equitantia, numerosa. Vernatio foliorum duplicativa. Species una adhuc nota, habitu *Acrolophiarum*.

Trichochilus neo-ebudicus Ames, sp. nov.

Radices valde incrassatae. Caules abbreviati, basibus foliorum omnino obtecti. Folia plus minusve equitantia, oblique erecta, longe triangularia, acuta, in sicco nervosa. Pedunculus elongatus gracilis, infra racemum paucibracteatus. Racemus laxus, plus minusve decemflorus. Flores membranacei, albidi, labello purpureo-tincto. Sepala lateralia oblongo-lanceolata, patentia. Sepalum dorsale simile. Petala oblongo-lanceolata. Labellum trilobatum, toto disco per medium inaequaliter pilosum et papillosum, basi saccatum vel breviter calcaratum; lobi laterales oblongi,

obtus; lobus medius anguste ovatus vel obovatus, obtusus, prope basim bicallosus callis papillosis, prope apicem crista pilosa ornatus. Columna elongata, incrassata, in pedem brevem producta. Pollinia duo, globosa.

Roots very stout, when dry about 5 mm. in diameter. Stem much abbreviated, about 1.5 cm. long, concealed by the equitant leaves. Leaves 1.5–4 cm. long, \pm 8 mm. wide, duplicative, persistent, narrowly triangular, acute, about 6, ascending with the apices curving inward toward the base of the elongated peduncle, conspicuously many-nerved when dry. Peduncle wand-like, slender, about 2 mm. in diameter when dry, about 5 dm. long, provided with about 5 tubular acute bracts below the raceme. Bracts 1–1.5 cm. long. Raceme about 10-flowered, 4–10.5 cm. long, about 4 cm. in diameter. Flowers about 5 mm. apart, white transfused with mauve. Bracts of the raceme 4–5 mm. long, narrowly lanceolate, acute, spreading, much shorter than the pedicels, brownish when dry. Pedicels about 1 cm. long, very slender, obliquely ascending. Ovary about 3 mm. long, arcuate. Lateral sepals 12–15 mm. long, 2.5 mm. wide, oblong-lanceolate, obtuse or subacute, membranaceous, forming a blunt mentum, 5-nerved with the outer nerves less conspicuous than the three middle ones. Upper sepal similar, about 12 mm. long. Petals about 12 mm. long, 3–3.5 mm. wide, similar to the sepals. Labellum about 11.5 mm. long, conspicuously 3-lobed, sharply deflexed near the base, forming a basal abbreviated sac or spur 1 mm. deep; lateral lobes hardly 3 mm. long, 1 mm. wide, oblong, obtuse, membranaceous, 2–3-nerved, divaricate; middle lobe about 8 mm. long, 3.5 mm. wide at the middle, narrowly ovate, obtuse, pubescent along the middle, contracted at base into an abbreviated oblong claw, bicallose at base with the calli extending down the claw, somewhat thickened at the slightly convex apical portion where it is densely covered with hairs. Calli densely pubescent. Column about 5.5 mm. long, fleshy, dilated upwards, produced at base into a short flat foot and with the base of the adherent labellum forming the short blunt sac. Pollina 2, spherical, waxy, each pollen mass supported by a slender elongated stipe. Stipes of the pollinia widely separated on the orbicular viscid disc.

NEW HEBRIDES. *Eromanga*; Cooks Bay, *Morrison*, s. n., July 22, 1896 (type in Herb. Kew.; duplicate of type in Herb. Ames, no. 37776); tableland, *Morrison*, s. n., July 16 & 22, 1896; Ulaveri plateau, *Morrison*, s. n., July 16, 1896; without exact location, *Morrison*, s. n., July 17, 1896; tableland of volcanic ash, among grass, and also among bracken, and at edge of belts of brush, altitude 500–700 feet, August 4, 1930, *L. Cheeseman*, no. 59.

It is clear that this species belongs to the subtribe Polystachyeae. Vegetatively it resembles *Acrolophia tristis* Schltr. & Bolus and *A. lamellata* Schltr. & Bolus, but is separable from them in the structure of the pollinarium, in the much shorter leaves, and through the absence of a conspicuous spur at the base of the labellum.

In the specimens studied the leaves are closely appressed to the base of the slender peduncle and are nearly parallel with it. Whether or not the leaves elongate as the plant matures is a question that cannot now be answered.

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SYNOPSIS OF THE CHINESE SPECIES OF JASMINUM

CLARENCE E. KOBUSKI

JASMINUM is essentially a tropical or subtropical genus and is found in eastern and southern Asia, Malaysia, Africa, Australia and even tropical America. There are probably over three hundred species recognized in the genus at the present time. In the herbarium of the Arnold Arboretum are represented species from all these regions. However, the region best represented is China. Of the few species not found in this herbarium, photographs of the type specimens were taken by Alfred Rehder on a recent visit to European botanical institutions from which he brought back over 500 photographs of types of Chinese ligneous plants. This gave us a nearly complete representation of the Chinese species of *Jasminum* and made possible the present study.

Since the time of Linnaeus there has been made only one attempt toward a complete representation of the genus; this was published in 1844 by A. P. De Candolle (*Prodr.* viii. 300-316). Of the Chinese species three enumerations were published, namely by Hemsley, Léveillé and Chung.

W. B. Hemsley (*Enumeration of all the Plants known from China proper, Formosa, Hainan, the Corea, the Luchu Archipelago and the Island of Hongkong*) in *Jour. Linn. Soc.* xxvi. 78-82 (1889) recognized fifteen species. H. Léveillé in handling his "*Jasmina Sinensia*" in *Fedde, Rep. Nov. Spec.* xiii. 149-150 (1914) mentions thirty-three species in his key while H. H. Chung publishing a "*Catalogue of Trees and Shrubs of China*" in *Mem. Sci. Soc. China*, i. no. 1 (1924) lists 27 species and two varieties.

As already mentioned in this paper there are over three hundred species. Early in the study we thought that most of these species were distributed in southeastern Asia and Malaysia and that here probably was the main center of distribution of the genus. However, in careful listing of all species of the genus as recognized by "*Index Kewensis*" we discovered that while there were approximately one hundred species of *Jasminum* found in China (especially south-west) and the Himalayan region of India there were about the same number of species found in Malaysia and about one hundred twenty species in Africa. Besides these numbers there is a sprinkling of a few species in Australia, Polynesia and tropical America. All together this makes the genus pan-tropical with a possible center of distribution found in the area including Malaysia, the Himalayas and China.

These numbers have been taken from species recognized by the Index Kewensis. Incidentally, of the fifty-six species belonging within the scope of this study approximately one-half turned out to be synonyms. No new species was found among the unidentified material either at the Arnold Arboretum or the material borrowed from other institutions. This may intimate that since *Jasminum* is composed mostly of such interesting and decoratively beautiful shrubs that the majority of species were found early by plant collectors and described at that time. It is evident that later botanists encountering some of these already described new species for the first time, lacking both material with which to compare them and literature, also have described several of the outstandingly distinct species a second and even a third time. At present, when the material (types or photographs of types) was brought together for the first time it was positively amazing to find the species duplications which had taken place.

One cannot be positive but it seems quite logical to assume that the same situation may be found in a study of *Jasminum* from any other distinct locality. This would decrease the number of recognized species considerably.

The genus is botanically separated quite easily into four distinct sections; the sections being based on leaf characters. These sections were all introduced by DeCandolle in his *Prodromus*. The *Alternifolia* group with alternately arranged leaves is perhaps the most outstandingly different. It contains five species and varieties. The opposite-leaved sections are three, namely: *Unifoliolata* (13 species); *Trifoliolata* (9 species and varieties); *Pinnatifolia* (5 species and varieties). The delimiting characters of these groups can easily be ascertained from their significant names.

In addition to the material in the herbarium of the Arnold Arboretum, photographs of types were secured and loans of material obtained from the herbaria of the New York Botanic Garden, the Philippine Bureau of Science, Gray Herbarium of Harvard University, Royal Botanic Garden at Edinburgh, British Museum of Natural History and Royal Botanic Gardens at Kew. Opportunity is taken at this time by the author to express his gratitude to all members of these institutions mentioned above who aided in photographic work or selection of the specimens loaned. Especial thanks are due Mr. Alfred Rehder, Curator of the Herbarium, for the suggestion of the problem and for the ever kind and helpful interest which has been shown me at all times during the progress of this work.

The abbreviations of the herbaria used in this paper are as follows:

- (AA) = Arnold Arboretum of Harvard University
 (B) = British Museum of Natural History
 (Br) = University of Breslau
 (C) = University of California
 (E) = Edinburgh, Royal Botanic Garden
 (G) = Gray Herbarium of Harvard University
 (K) = Kew, Royal Botanic Gardens
 (NY) = New York Botanical Garden
 (P) = Philippine Bureau of Science

KEY TO THE SERIES

- A. Leaves alternately arranged.....1. ALTERNIFOLIA
 AA. Leaves opposite in arrangement.
 B. Leaves compound.....2. TRIFOLIOLATA
 C. Leaves trifoliolate.....2. TRIFOLIOLATA
 CC. Leaves five-foliolate or more.....3. PINNATIFOLIA
 BB. Leaves simple.....4. UNIFOLIOLATA

Series 1. ALTERNIFOLIA DC.

- A. Calyx teeth subulate-setaceous, longer than calyx-tube.
 B. Leaves and plant glabrous.....1. *J. floridum*
 BB. Leaves puberulous.....2. *J. Giraldui*
 AA. Calyx lobes shorter than calyx-tubes, diminutive or obtuse.
 B. Leaves both simple and ternate; leaflets 5-8 cm. long; inflorescence
 30-50-flowered, corymbs 7-12 cm. across.
 C. Calyx lobes and pedicels glabrous.
 3a. *J. heterophyllum* var. *glabricorymbosum*
 CC. Calyx lobes and pedicels villous.
 3b. *J. heterophyllum* var. *subhumile*
 BB. Leaves only ternate or pinnate; leaflets 1.5-3.5 cm. long; inflorescence
 3-8 flowered.....4. *J. humile*

1. *Jasminum floridum* Bunge in Mém. Div. Sav. Acad. Sci. St. Pétersb. II. 116 (Enum. Pl. China Bor. 42) (1833).—DeCandolle, Prodr. VIII. 313 (1844).—Nicholson, Ill. Dict. Gard. II. 207 (1877).—Miquel in Ann. Mus. Ludg.-Bat. II. 263 (1866); Prol. Fl. Jap. 151, 359 (1866-67).—Franchet & Savatier, Enum. Pl. Jap. I. 314 (1875).—Hooker f. in Bot. Mag. CIX. t. 6719 (1883).—Hemsley in Jour. Linn. Soc. XXVI. 78 (1889).—Diels in Bot. Jahrb. XXIX. 534 (1900).—Schneider, Ill. Handb. Laubholzk. II. 839, figs. 527h-i, 528a (1911).—Léveillé in Fedde, Rep. Spec. Nov. XIII. 149 (1914).—Rehder in Sargent, Pl. Wilson. II. 614 (1916); Man. Cult. Trees Shrubs, 765 (1927).—Chung in Mem. Sci. Soc. China, I. no. 1, 216 (1924).

Jasminum subulatum Lindley in Bot. Reg. XVIII. misc. notes, 57 (1842).—DeCandolle, Prodr. VIII. 312 (1844).

Jasminum floridum Bunge var. *spinescens* Diels in Bot. Jahrb. XXIX. 534 (1901).—Syn. nov.

Jasminum Argyi Léveillé in Mem. Acad. Ci. Art. Barcelona, XII. no. 22, 17 (1916).—Syn. nov.

Chihli: Peking, *C. A. Skatchkov* (1848-1857) (G). **Kiang-su:** Le kien, *Ch. d'Argy*, May (1846-66) (AA, type of *J. Argyi*); Nanking, *L. F. Tsu*, no. 629, May 19, 1921 (C). **Western Hupeh:** north and south of Ichang, alt. 300-700 m., *E. H. Wilson*, no. 789 in part, June and December 1907 (bush 1 m. tall; flowers yellow; fruit black) (AA, G); open, grassy slopes, Ichang, *W. Y. Chun*, no. 3468, July 20, 1922 (bush 1 m. high; flowers yellow) (AA); thickets, Hsing-shan hsien, alt. 600 m., *E. H. Wilson*, no. 789 in part, June 1907 (AA); moist shady cliff, Gian Gia-kou, *W. Y. Chun* (*Huang Tsung*), no. 3572, July 27, 1922 (shrub 1-2 m.; leaves dull green above; flowers yellow) (AA); without precise locality, *E. H. Wilson* (Veitch Exped. no. 83) April 1900 (AA, NY); without precise locality, *A. Henry*, nos. 2700 (NY, G) and 6288 (AA, NY). **Kansu:** near Kua tsa, *F. N. Meyer*, no. 1817, Nov. 5, 1914 (C). **Western Szechuan:** Nanch'uan, *Fu pei tsui*, *C. Bock* and *A. von Rosthorn*, no. 1151, Oct. 1891 (photo. and fragment of holotype of *J. floridum* var. *spinescens*) (AA); Nanch'uan, Taho-kou, *C. Bock* and *A. von Rosthorn*, no. 163, July 1891 (AA); side of river, Nanchuan hsien, alt. 1525-1830 m., *W. P. Fang*, no. 788, May 15, 1928 (shrub 1 m.; flowers yellow) (AA, NY); side of brook, Sungpan hsien, *W. P. Fang*, no. 4239, August 17, 1928 (shrub 2-3 m.; flowers yellow) (AA, NY).

In comparing *J. Argyi* Léveillé with material of *J. floridum* Bunge, no differences warranting specific delimitation could be found, nor does *J. floridum* var. *spinescens* Diels seem to be different enough from typical *J. floridum* to be maintained as a distinct variety.

2. *Jasminum Giraldii* Diels in Bot. Jahrb. xxix. 534 (1901).—Pampanini in Nuov. Giorn. Bot. Ital. n. ser. xvii. 689 (1910).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 149 (1914).—Bailey, Standard Cycl. Hort. 1719 (1915).—Rehder in Sargent, Pl. Wilson. ii. 614 (1916); Man. Cult. Trees Shrubs, 765 (1927).—Chung in Mem. Sci. Soc. China, i. no. 1, 216 (1924).

Jasminum tsinlingense Lingelsheim in Fedde, Rep. Spec. Nov. Beih. xii. 463 (1922).—Syn. nov.

Shensi: King lung shan, alt. 900 m., *J. Hers*, no. 2440, Oct. 9, 1922 (AA); In kia p'u, *G. Giraldi*, no. 1518, August 1897 (fragment of syntype from Herb. Mus. Berlin) (AA); Huo kia zaez, at foot of Lao y huo, *G. Giraldi*, no. 1519 (photograph of syntype in Herb. Mus. Berlin) (AA); same locality, June 4, 1897, *G. Giraldi* (AA); northwest of Hangcheng hsien, *W. Purdom*, no. 368, date lacking (1 m. high; flowers yellow) (AA); Tai-pei-shan, *W. Purdom*, nos. 907 and 908, in 1910 (AA); at foot of mts. at Schian gou, south Hsian fu, Tsin ling schan, alt. 500 m., *W. Limpricht*, no.

2689 (photograph and fragment of type of *J. tsinglingense* from Br. in AA). H u p e h : dry rocky places, Fang hsien, alt. 1000 m., *E. H. Wilson*, no. 598, May 23, and Nov. 1907 (abundant; 1-2 m.; flowers deep yellow; fruit black) (AA, G, NY, C).

Lingelsheim's species *Jasminum tsinglingense* is undoubtedly synonymous with *J. Giraldii* Diels.

3a. *Jasminum heterophyllum* Roxb. var. *glabricorymbosum* W. W. Smith in Notes Roy. Bot. Gard. Edinburgh, XII. 209 (1920).

Y u n n a n : on ledges of limestone cliffs, on Langhong—Hoching divide, lat. 26° 16' N., alt. 2440 m., *G. Forrest*, no. 9990, May 1913 (shrub 2-3 m.; flowers deep golden yellow, fragrant) (AA); in open situations by streams, Yungpe mountains, lat. 26° 45' N., alt. 2740 m., *G. Forrest*, nos. 11037 (NY), 11177 (C), and 11472, Sept.-Oct. 1913 (erect shrub 2-2.5 m.; fruit black) (AA); Mengtze woods, alt. 1475-1525 m., *A. Henry*, nos. 9107, 9107A and 9107B (slender shrubs 2-2.5 m.; flowers yellow; fruit black) (AA, NY); forests, Ta Song pin, *Simeon Tén*, no. 99, March 26, 1916 (tree 3 m.; flowers yellow) (AA); eastern slopes of Likiang Snow Range, Yangtze watershed, Prefectural District of Likiang, *J. F. Rock*, nos. 3879, 3955, May-Oct. 1922 (shrub 2-2.5 m.; flowers orange-yellow) (AA, NY); mountains south of Likiang Sungkwe Hochin Range, *J. F. Rock*, no. 8292 in 1923 (shrub 1.5-2 m.; flowers yellow) (AA); western slope of Likiang Snow Range, Yangtze watershed, *J. F. Rock*, no. 8539 April 1923 (shrub 3 m.; drooping yellow flowers) (AA); banks of Djiper Ka Ku stream, near Ngaza, drainage basin of the Yangtze, west of Likiang, *J. F. Rock*, no. 10602, in 1923 (shrub 1 m.) (AA); Shweli River drainage basin and environs of Tengyueh, *J. F. Rock*, no. 8033, February 1923 (shrub 1.2-2 m.; flowers citron-yellow) (AA); headwaters of the Red River or Menghuaho from Maokai to Tatsang, alt. 1675 m. *J. F. Rock*, no. 3026, April 8, 1922 (flowers yellow) (AA).

3b. *Jasminum heterophyllum* Roxb. var. *subhumile* (W. W. Smith), comb. nov.

Jasminum subhumile W. W. Smith in Notes Bot. Gard. Edinb. VIII. 127 (1913).

Y u n n a n : moist open situation in the Sha-Yang valley, lat. 25° 20' N., alt. 1830 m., *G. Forrest*, no. 5529, April 1910 (flowers orange-yellow, fragrant) (E, type of *J. subhumile*); open situation in the Pu-piao valley, lat. 25° '5 N., alt. 1830-2135 m., *G. Forrest*, no. 9873, May 1913 (shrub 1.5-3 m.; flowers deep golden yellow, fragrant) (AA, C).

This variation of *J. heterophyllum* was originally described as *J. subhumile*. However, it differs from *J. heterophyllum* only in

its densely villous pubescence found on the calyx and pedicels. The pubescence on *J. heterophyllum* is of a puberulent nature. It is interesting to find these two extreme variations, namely the present villous variety along with the glabrous variety mentioned before both growing in China, while the typical species has been found only in the Himalayan region.

4. *Jasminum humile* Linnaeus, Spec. Pl. i. 7 (1753).—Aiton, Hort. Kew. i. 9 (1789).—Ker in Bot. Reg. v. t. 350 (1819).—St. Hilaire, Pl. France, ii. t. 110 (1808); Traité Arbriss. & Arbustes, ii. t. 90 (1825).—DeCandolle, Prodr. viii. 313 (1844).—Clarke in Hooker f., Fl. Brit. Ind. iii. 602 (1822).—Nicholson, Illustr. Dict. Gard. ii. 207 (1887).—Dippel, Handb. Laubholz. i. 146, fig. 91 (1889).—Bailey, Cyclop. Amer. Hort. ii. 843, fig. 1191 (1900); Stand. Cyclop. Hort. iii. 1719, fig. 209 (1915).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 149 (1914).—Brandis, Ind. Trees, 452 (1906).—Schneider, Ill. Handb. Laubholz. ii. 840 (1911).—Rehder in Sargent, Pl. Wilson. ii. 615 (1916); Man. Cult. Trees Shrubs, 765 (1927).—Chung in Mem. Sci. Soc. China, i. no. 1, 216 (1924).—Boynton in Addisonia, xii. 55, pl. 412 (1927).

Jasminum chrysanthemum Roxburgh, Cat. Hort. Beng. 3 (1814), nomen; Fl. Ind. i. 98 (1820).

Jasminum revolutum Sims in Bot. Mag. xlii. t. 1731 (1815).—Ker in Bot. Reg. iii. t. 178 (1817); vi. notes 2 (1820).—Loddiges in Bot. Cab. x. t. 966 (1824).—D. Don, Prodr. Fl. Nepal. 106 (1825).—De Candolle, Prodr. viii. 313 (1844).—Wight, Icon. Pl. Ind. Orient. iv. 14, t. 1258 (1850).—Brandis, Forest Fl. Brit. Ind. 313 (1874).—Boissier, Fl. Orient. iv. 42 (1879).—Dippel, Handb. Laubholz. i. 148, fig. 93 (1889).—Schneider, Ill. Handb. Laubholz. ii. 839, figs. 527 m-n, 528 g-i (1911).

Jasminum bignoniaceum Wallich, Cat. No. 2888 (1829), nomen nudum.—G. Don, Gen. Syst. iv. 63 (1838).—DeCandolle, Prodr. viii. 313 (1844).

Jasminum Wallichianum Lindley in Bot. Reg. xvii. t. 1409 (1831).—Schneider, Ill. Handb. Laubholz. ii. 839, figs. 527 k-l, 528 d-f (1911).

Jasminum inodorum Jacquemont apud Decaisne in Jacquemont, Voy. iv. 139. t. 143 (1844).—DeCandolle, Prodr. viii. 312 (1844).

Jasminum Mairei, Léveillé in Fedde, Rep. Spec. Nov. xiii. 337 (1914).—Syn. nov.

Jasminum Mairei Léveillé var. *siderophyllum* Léveillé, Cat. Pl. Yun-nan, 179 (1916).—Syn. nov.

Kansu: Lower Tebbu country: slopes along gorge of Chulungapu, alt. 1980 m., *J. F. Rock*, no. 15035, Sept.-Oct. 1926 (shrub 1-1.7 m.; flowers yellow; fruit black) (AA); dry arid slopes with Oaks in Nyibaku, alt. 1900 m., *J. F. Rock*, no. 14797, Sept. 9, 1926 (shrub 1-1.5 m.; flowers rich yellow) (AA); outskirts of forests along stream in Wantsang valley, alt. 2135-2200 m., *J. F. Rock*, no. 14653, Aug. 31, 1926 (shrub 1-1.5 m.) (AA). Western Szechuan: descent of Hsao-chin-lo, Monkong Ting,

alt. 2300–3000 m., *E. H. Wilson*, no. 2809, June 1908 (bush 1–2 m. tall; flowers yellow) (AA); dry arid places, Maochou, alt. 1300–1600 m., *E. H. Wilson*, no. 2811, May 24, 1908 (bush 0.3–2 m. tall; flowers yellow) (AA); in dumetis mont., inter Kalapo et Linku, alt. 3000 m., *C. K. Schneider*, no. 1302, May 17, 1914 (AA); inter Huale et Mo lien, alt. 2600 m., *C. K. Schneider*, no. 4091, May 25, 1914 (AA); Teng-hsiang-ying, alt. 2100 m., *Harry Smith*, no. 1890, May 20, 1922 (in prato fruticoso-herboso) (AA); inter Wen-ch'uan-hsien et Hsin-p'u-kuan, alt. 1300 m., *Harry Smith*, no. 2463, June 28, 1922 (flor. sulphurei) (AA); without exact locality, alt. 3000–3300 m., *E. H. Wilson* (Veitch Exped. no. 4077) June 1904; alt. 2300 m., *E. H. Wilson* (Veitch Exped. no. 4078) August 1903 (AA). Y u n n a n : high plateau between Talifu and Likiang to the foot of the Likiang Snow Range, *J. F. Rock*, no. 3293, May 6–11, 1922 (shrub; flowers yellow) (AA); about Pe Yen tsin, *Simeon Tén*, no. 515, June 18, 1918 (shrub 1–2 m.) (AA); Pin tchoan kai, about Pe Yen tsin, *Simeon Tén*, no. 375, May 15, 1917 (spreading shrub 1–2 m.; flowers yellow) (AA); open situation on arid foothills of eastern flank of Bei-ma Shan, lat. 28° 12' N., alt. 3050 m., *G. Forrest*, no. 13832, June 1917 (shrub 1–2 m.; flowers deep golden yellow) (AA); vallons de Suen-oui, alt. 2400 m., *E. E. Maire* (AA, no. 451), July (arbrisseau buissonnant; fleurs jaunes) (AA); vallée de Gui-ma-tong, alt. 2500 m., *E. E. Maire* (AA, no. 245) May (arbuste buissonnant non grim pant; fleurs jaunes) (AA); open situation in mixed and pine forests on the eastern flank of the Tali Range, lat. 25° 40' N., alt. 2440–3050 m., *G. Forrest*, no. 4659, June–August 1906 (shrub 1–2 m., flowers orange-yellow, fragrant) (AA); in calcareous mountains, region of Yunnan fu, alt. 2200 m., *O. Schoch*, no. 36 (AA); in hedges near Hoching, alt. 2500 m., *C. K. Schneider*, no. 3264, Sept. 26, 1914 (AA); in thickets near streams at foot of mountain near Lichiang, alt. 3000 m., *C. K. Schneider*, no. 3222, Oct. 6, 1914 (AA); haut plateau de Tai hai, alt. 3200 m., *E. E. Maire*, July (1911–13) (arbuste buissonnant; haut 0.60 m.; fleurs roses) (AA); pâturages des montagnes à Pe-ling-tsin, alt. 3200 m., *E. E. Maire*, May (1911–13) (buissonnant, haut 0.60 m.; fleurs jaunes, inodores) (AA). S o u t h e a s t T i b e t : open scrub by streams on the Salween-Kiu-chiang divide, Tsarong, lat. 28° 40' N., long. 98° 15' E., alt. 2135–2440 m., *G. Forrest*, no. 18927, September 1919 (shrub 1–2 m.) (AA); amongst rocks on dry stony slopes in side valleys on the Salween-Kiu-chiang divide, Tsarong, lat. 28° 40' N., long. 98° 15' E., alt. 2440 m., *G. Forrest*, no. 19251, September 1919 (shrub 0.5 m.) (AA).

In examining the Indian along with the Chinese material, one, at first, is impressed with the seeming differences and inclined to recognize the species *J. revolutum* Sims and *J. Wallichianum* Lindley as distinct from *J. humile* L. This separation would be based on the larger, more numerous and rather obtuse leaflets of the Indian material as compared with the small, acute, and lesser numbered leaflets of the Chinese species. The number of flowers in the inflorescence of the Himalayan material is greater (usually 8-10) as contrasted with the usual 3-5-flowered inflorescence of the Chinese specimens. On careful study of the massed material, however, one finds a sufficiently distinct graduation or variation in all the characters mentioned making it difficult to recognize anything other than a single, very variable species, *J. humile*.

Series 2. TRIFOLIOLATA DC.

A. Calyx lobes foliaceous.

B. Leaves persistent, coriaceous, present at time of flowering

5. *J. Mesnyi*

BB. Leaves deciduous; flowers appearing before leaves.

C. Plants erect or scandent; simply branched.

D. Leaves uniformly green.....6. *J. nudiflorum*

DD. Leaves variegated or entirely yellow..6a. *J. nudiflorum* f. *aureum*

CC. Plants pulvinate; intricately ramose.

6b. *J. nudiflorum* var. *pulvinatum*

AA. Calyx lobes quite vestigial or subulate when present.

B. Leaves palmately tri-nerved.

C. Branchlets and leaves glabrous.....7. *J. urophyllum*

CC. Branchlets and leaves puberulent..7a. *J. urophyllum* var. *Wilsonii*

BB. Leaves pinnately veined.

C. Leaves and branches glabrous.....8. *J. lanceolarium*

CC. Leaves and branches pubescent.

D. Calyx lobes quite vestigial; terminal leaflets same size or only slightly larger than lateral leaflets

8a. *J. lanceolarium* var. *puberulum*

DD. Calyx lobes subulate-setaceous; terminal leaflets markedly longer than lateral leaflets.....9. *J. sinense*

5. *Jasminum Mesnyi* Hance in Jour. Bot. xx. 37 (1882).—Hemsley in Jour. Linn. Soc. London, xxvi. 79 (1889).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 150 (1914).—Chung in Mem. Sci. Soc. China, i. 216 (1924).

Jasminum primulinum Hemsley apud Baker in Kew Bull. Misc. Inform. 1895, p. 109; apud Oliver in Hooker, Ic. Pl. xxiv. t. 2384 (1895).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 150 (1914).—Bailey, Stand. Cyclop. Hort. iii. 1713 (1915).—Chung in Mem. Sci. Soc. China, i. 216 (1924).—Rehder, Man. Cult. Trees Shrubs, 764 (1927).—Syn. nov.

Y u n n a n : between Szemao and Nakoli, *J. F. Rock*, no. 2829, March 13, 1922 (shrub with straggling branches; flowers yellow) (AA); mountains near Szemao, alt. 1525 m., *A. Henry*, no. 9319A (straggly shrub with yellow flowers) (AA, C); brousse de montagne à Siao-long-tan, alt. 2600 m., *E. E. Maire*, AA, no. 199, April?

(arbuste en touffes, long rameaux verts; fleurs jaunes, simples ou doubles) (AA); dumetis ad vicum Dschung-duilung, prope urbem Yunnanfu, alt. 2000 m., *H. Handel-Mazzetti*, no. 8613, February 7, 1916 (flores flavi) (AA); an Bahn bei Yi leang hien, *C. K. Schneider*, no. 32, Feb. 5, 1914 (AA); westlich von der Yangtze Fähre, La ka tiang, *C. K. Schneider*, no. 486, March 19, 1914 (niederliegender sparriger Strauch) (AA); Mengtze, alt. 1370–1525 m., *A. Henry*, no. 9319 (shrub 1 m., flowers yellow) (AA, NY); amongst scrub, hills to the south of Tengyueh, lat. 25° N., alt. 1830 m., *G. Forrest*, no. 9744, March 1913 (shrub 1.5 m.; flowers bright golden yellow) (AA); dry rocky situation on the Langkong-Hoching divide, lat. 26° 16' N., alt. 2440–2740 m., *G. Forrest*, no. 9955, May 1913 (shrub 0.5–1.0 m., flowers golden yellow) (AA); Yunnan fu, in fruticetis, alt. 1900 m., *Harry Smith*, no. 1583, August 4, 1922 (AA); precise locality and date lacking, *F. Ducloux*, nos. 165, 7175 (NY). Kweichow: prope Mei-chu-chin, alt. 1830 m., *W. Mesny* (Hance herb. no. 21211), April 11, 1880, (B, type), photo. of type (AA).

Unfortunately in describing *J. primulinum*, Hemsley (1895) was not aware of *J. Mesnyi* described by Hance in 1882. Since Hemsley's time this species has been known generally as *J. primulinum* instead of the earlier name *J. Mesnyi*.

J. Mesnyi seems to be the southern counterpart of *J. nudiflorum*. It is difficult to find sound morphological characters for specific delimitation. *J. nudiflorum* is confined (spontaneously) to N. China and is characterized by deciduous leaves and precocious flowers with the corolla tube longer than the spread of its lobes. *J. Mesnyi*, on the other hand, is usually found in Yunnan and differs from *J. nudiflorum* in having evergreen leaves and larger, usually double flowers with the corolla-lobe spread greater than the length of the tube.

6. *Jasminum nudiflorum* Lindley in Jour. Roy. Hort. Soc. London, i. 153 (1846); Bot. Reg. xxxii. t. 48 (1846); Bot. Mag. lxxxviii. t. 4649 (1852).—Walpers, Repert. Bot. Syst. vi. 463 (1846–47).—Franchet, Pl. David. i. 206 (1884).—Hemsley in Jour. Linn. Soc. London, xxvi. 79 (1889).—Schneider, Ill. Handb. Laubholz. ii. 837 (1912).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 150 (1914).—Bailey, Stand. Cyclop. Hort. iii. 1718 (1915).—Chung in Mem. Sci. Soc. China, i. 216 (1924).—Rehder, Man. Cult. Trees Shrubs, 764 (1927).

Jasminum angulare Bunge in Mém. Div. Sav. Acad. Sci. St. Pétersb. ii. 116 (Enum. Pl. China Bor. 42) (1833).—Non Vahl.

Jasminum Sieboldianum Blume, Mus. Bot. Ludg.-Bat. i. 280 (1850).

S h a n s i : Yun-cheng, Chung-t'iao-shan, in prato aprico, *Harry Smith (Ssii Ho)*, no. 5508, July 1924 (AA). S h a n t u n g : Tsingtao, *R. Zimmermann*, no. 296 in 1901 (AA); along sandy slope under partial shade, Tsingtao, alt. 100 m., *C. Y. Chiao*, no. 2583, June 19, 1930 (bushy vine, ornamental for stone walls) (AA).

6a. *Jasminum nudiflorum* Lindley f. *aureum* Dippel, Handb. Laubholz. i. 145 (1889), as var.—Schneider, Ill. Handb. Laubholz. ii. 837 (1912), as var.

J. nudiflorum Lindley var. *variegatum* Mouillefert, Arbres Arbriss. ii. 1008 (1897).

Hort. L. Spaeth, Baumschulen, Berlin, Aug. 8, 1926 (leaves yellow, green and variegated); same location, *H. Jensen*, in flower, March 21 (1927).

6b. *Jasminum nudiflorum* Lindley var. *pulvinatum* (W. W. Smith), comb. nov.

Jasminum pulvinatum W. W. Smith in Notes Roy. Bot. Gard. Edinb. xii. 209 (1920).

S . E . T i b e t : in open dry situations on cliffs, prov. of Tsarong, on Doker-la, Mekong-Salween divide, lat. 28° 20' N., alt. 2740–3050 m., *G. Forrest*, no. 14478, July 1917 (cushion shrub of 0.25–0.5 m.; flowers golden yellow) (AA). N . W . Y u n n a n : mountains of Londjre, Mekong-Salween watershed adjoining southeastern Tibet, *J. F. Rock*, no. 8896, May 1923 (shrub 0.25–0.5 m. often prostrate; flowers large rich yellow) (AA, NY); on open moorland, eastern flank of the Bei-ma Shan, lat. 28° 12' N., alt. 4250–4500 m., *G. Forrest*, no. 13834, July 1917 (stunted, almost spinous shrub, 0.25 m.; flowers bright yellow) (AA); dry situations in ravines in the Salween valley, lat. 28° 10' N., alt. 2440 m., *G. Forrest*, no. 16193, April 1917 (shrub 0.75–1.5 m.; flowers precocious, bright yellow) (AA); stony pasture and on cliffs on the Bei-ma Shan, lat. 28° 18' N., long. 99° 10' E., alt. 3650–3950 m., *G. Forrest*, no. 19666, July 1921 (matted cushion shrub of 0.3–0.75 m; flowers yellow) (AA); on ledges of dry cliffs and rocky slopes in the Atuntze valley, lat. 28° 32' N., long. 98° 48' E., alt. 2740–3050 m., *G. Forrest*, no. 20004, August 1921 (stunted shrub 0.3–0.75 m. forming cushions; flowers bright yellow) (AA).

This stunted variety of *J. nudiflorum* Lindl. found growing, as far as is known at present, only in the mountainous regions of N. W. Yunnan and adjacent S. E. Tibet varies from the species *J. nudiflorum* in the cushion like habit and densely intricate branching. It is solely an alpine equivalent of *J. nudiflorum* and not worthy of specific rank.

7. *Jasminum urophyllum* Hemsley in Jour. Linn. Soc. Bot. xxvi. 81 (1889).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 150 (1914).—

Rehder in Sargent, Pl. Wilson. II. 613 (1916).—Chung in Mem. Sci. Soc. China, I. 217 (1924).

Szechuan: Mt. Omei, alt. 1525 m., *Ernst Faber*, no. 47 (flowers yellow) (NY, isotype); in thickets, Kuan hsien, alt. 900–1080 m., *W. P. Fang*, no. 2196, July 14, 1928 (woody vine; flowers white) (AA, NY); in thickets near Mt. Wa, alt. 900 m., *E. H. Wilson*, no. 1122, Oct. 1908 (climber, 2 m.; flowers white) (AA).

An annotation found on the sheet of the type specimen of this species refers to the flowers as yellow. In view of the facts that all other specimens of this species and its variety possess white flowers and that the plant at time of collection from which the type specimen was gathered was evidently nearly past the flowering condition, I feel that, probably, the original specimen possessed white flowers which, because of their aged condition, were termed yellow.

J. urophyllum is closely allied to the Indian *J. dispersum* Wall. in its white flowers, ternately-veined leaflets and calyx characters. However, the two lateral veins in *J. urophyllum* pass well beyond the center toward the apex of the leaf before anastomosing with the small veinlets from the midrib while in the case of *J. dispersum* the veins anastomose well below the center of the leaf. Also the leaves of *J. dispersum* are more vigorous, 5-foliate and coarser in texture while those of *J. urophyllum* are narrowed and more attenuated, 3-foliate and finer in texture.

7a. *Jasminum urophyllum* Hemsley var. *Wilsonii* Rehder in Sargent, Pl. Wilson. II. 613 (1916).—Chung in Mem. Sci. Soc. China, I. 217 (1924).

Jasminum urophyllum Hemsley var. *Henryi* Rehder in Sargent, Pl. Wilson. II. 613 (1916).—Chung in Mem. Sci. Soc. China, I. 217 (1924).—Syn. nov.

W. Szechuan: cliffs, *E. H. Wilson*, Veitch Exp. no. 4075, July 1903 (shrub 0.6 m. high; flowers white) (AA, type). W. Hupeh: Mt. Changyang, *E. H. Wilson*, Veitch Exp. no. 1499, July 1900 (climber with white flowers) (AA, NY; paratype of var. *Henryi*); Yunnan: on and amongst scrub, divide between the Shweli and Tengyueh valleys, lat. 25° N., alt. 2135 m., *G. Forrest*, no. 8136, June 1912 (scandent shrub 1.5–4.5 m.; flowers, interior ivory-white, exterior flushed rose-crimson, fragrant) (AA).

This variety of *J. urophyllum* is quite distinct and easily recognized from the typical species because of the absence of the pubescent character so prominent in *J. urophyllum*. The variety *J. urophyllum* var. *Henryi* cannot be clearly distinguished from var. *Wilsonii* and was evidently described from rather sparse material.

8. *Jasminum lanceolarium* Roxburgh, Fl. Ind. i. 97 (1820).—DeCandolle, Prodr. viii. 310 (1844).—C. B. Clarke in Hooker f., Fl. Brit. Ind. iii. 601 (1882).—Hemsley in Jour. Linn. Soc. xxvi. 78 (1889).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 150 (1914).—Rehder in Sargent, Pl. Wilson. ii. 612 (1914).—Chung in Mem. Sci. Soc. China, i. 216 (1924).

Jasminum paniculatum Roxburgh, Fl. Ind. i. 97 (1820).—Ker in Bot. Reg. ix. t. 690 (1823).—DeCandolle, Prodr. viii. 310 (1844).—Bentham in Fl. Hongkong, 216 (1861).—Hemsley in Jour. Linn. Soc. xxvi. 80 (1890).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 150 (1914).—Chung in Mem. Sci. Soc. China, i. 216 (1924).—*Syn. nov.*

Jasminum discolor Franchet in Nouv. Arch. Mus. Paris, sér. 2, x. 59 (1888).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 150 (1914).—Chung in Mem. Sci. Soc. China, i. 216 (1924).—*Syn. nov.*

Jasminum pachyphyllum Hemsley in Jour. Linn. Soc. xxvi. 79 (1890).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 150 (1914).—Chung in Mem. Sci. Soc. China, i. 216 (1924).—*Syn. nov.*

A n h w e i : in open thickets, E. Wu Yuan, alt. 540 m., *R. C. Ching*, no. 3312, September 4, 1925 (strong, tough climber, 15 m.; bark dark gray, green above, fruit greenish, rounded) (AA). K i a n g s i : shady valley near stream, Ting-Nan hsien, alt. 690 m., *H. H. Hu*, no. 1065, June 5, 1921 (vine with white flowers) (AA). K w a n t u n g : Lantau Island (native collector ex *C. Ford*) May 11, 1888 (AA, photo. of type of *J. pachyphyllum*); Hongkong, *C. Ford*, Nov. 22, 1893 (AA); precise locality lacking, *C. Ford*, August 9, 1895 (NY); Hongkong, *C. Wright*, in 1853-1856 (NY); Teng Woo Mt., *C. O. Levine* and *G. W. Goff*, no. 163, Nov. 18, 1916 (C); same locality, *C. O. Levine*, no. 3107, Sept. 22, 1918 (AA); Loh Fan Mountain, *E. D. Merrill*, no. 10693, August 9-27, 1917 (C, NY); Wong Nei Chong, Hongkong, *Y. Tsiang*, no. 3005, August 1929 (NY); Wukantin, Hongkong, New Territory, *Y. Tsiang*, no. 2970, August 1929 (NY); Tai-O, *Y. K. Wang*, no. 3206, August 1929 (NY); Tai-P, Hongkong, New Territory, *Y. K. Wang*, no. 3219, August (1929) (NY); open scrub, Tai-O, *W. Y. Chun*, no. 3088, August 17, 1929 (scandent shrub; leaves lustrous green; flowers yellow?) (NY); dense woods in partial shade, Sha-ting, Hongkong, *W. Y. Chun*, no. 6911, December 3, 1928 (scandent) (NY); dense woods, side of trail, Forestry Road above Bowen Road, Hongkong, *W. Y. Chun*, no. 7470, September 11, 1929 (scandent shrub; branches purple; leaves deep, dull green above, pale yellow green beneath; flowers white) (NY); Lan Tau Island, *Tsang Wai Tak*, no. 16718 (C); prope vicum Fotsaogai in medio inter urbes Kanton et Lienping situm, alt. 400 m., *R. Mell*, no. 62, Jan. 2, 1920 (scandens; fr. lignosi brunnei) (AA). K w a n g s i : 15 li south of Nee Bai, border of Kweichow, *R. C. Ching*, no. 6282, June 29, 1928 (AA, NY); Tsin-hung-shan, N. Hin-yen, *R. C.*

Ching, no. 6954, August 18, 1928 (AA). Western Szechuan : in thickets, Ya-chou, alt. 600-900 m., *E. H. Wilson*, no. 781, July & Dec. 1908 (climber, 5 m.; flowers white) (AA, G); Mt. Omei, *E. H. Wilson*, Veitch Exp. no. 5042, July 1904 (AA); in thickets, Nanchuan hsien, *W. P. Fang*, no. 5666, Oct. 30, 1928 (AA, NY). Yunnan : between Man-pieh and Man Lien, *J. F. Rock*, no. 2934, March 21, 1922 (scandent shrub with stiff, drooping branches; flowers white; fruits purple) (AA); beyond Lung Kai, watershed of Black River, or Papienho, *J. F. Rock*, no. 3069, April 5, 1922 (scandent shrubs with very fragrant, white flowers) (AA); between Tengyueh and Bhamo at the Yunnan-Burma border, *J. F. Rock*, no. 7833, December 1922 (scandent shrub) (AA); Mengtze, *A. Henry*, no. 940, Dec. 20 (shrub 1.5 m.) (NY); Szemao forests, alt. 1525 m., *A. Henry*, no. 11713 (large climber on trees; white flowers) (AA, NY); on scrub in thickets, hills east of Tengyueh, lat. 25° N., alt. 1830-2135 m., *G. Forrest*, no. 8072, June 1912 (scandent shrub 1.5-3.5 m.; flowers ivory-white, exterior dull crimson-lake, strongly fragrant) (AA); in open situations on trees in the Machang-kai valley, lat. 25° 30' N., alt. 2135 m., *G. Forrest*, no. 11827, July 1913 (scandent shrub 3.5-6 m.; flowers waxy white, flushed rose exterior, fragrant) (AA). Annam : in thickets along river, Tourane, *J. & M. S. Clemens*, no. 3448, May-July 1927 (vine) (AA). Assam : jungle near Naga Hill, *Dr. D. Prain's collector*, no. 892, April 1899 (AA); Mausmai, Khasia and Jaintia Hills, alt. 1220 m., *L. F. Ruse*, no. 135, May 18, 1923 (shrubby climber, 6 m.; flowers white) (AA).

At first this species seemed a rather troublesome problem on account of its close relationship with *J. paniculatum* Roxb. and *J. pachyphyllum* Hemsley and the difficulty of definitely limiting any of the species.

Roxburgh in *Flora Indica* described both *J. lanceolarium* and *J. paniculatum*. The description of *J. lanceolarium* came first, was rather brief and signified only that the leaves were lanceolate and the "corymbs" terminal. Corymbs as used here proved to be an unfortunate term because all the species have open panicles. They often appear as corymbs because of the size and compactness of the flower clusters. Immediately following came the description of *J. paniculatum*. In this species "the leaflets are from oval to oblong with an obtuse point, polished and of hard texture. The flowers are small and white but numerous, on terminal pretty large open, brachiate panicles." These descriptions are both so very brief that no clue to the real identity of a plant can be had.

As a further complication, Hemsley later described the species

J. pachyphyllum which supposedly varied from "*J. paniculatum* which has narrower leaflets and distinctly pedicellate flowers." However, we have at hand material from the same locality, agreeing with Hemsley's description but possessing distinctly lanceolate leaves.

Fortunately we have sixty or more specimens of these three species in question. Included among them is an excellent photograph of the type of *J. pachyphyllum* and material collected from the type localities of the other species. At first, one is in a quandary just how to separate the species and draw a line of demarkation. The ample material at hand proved to be a salvation because it definitely proved that no distinct line can be drawn between these three species.

The greatest variation factor is leaf form. Here we find the gradation from distinctly lanceolate through ovate or elliptic-lanceolate to distinctly rotund or obtusely apiculate leaves. Furthermore these variations are found throughout the whole geographical range and not limited to individual regions which fact makes the retention of leaf forms as geographical varieties quite unadvisable. The geographical range is rather pronounced, extending from Assam and Indo-China north through all the provinces of China except those of northern China. However the series of gradation and intergradation of the characters used in limiting these species is so gradual and definitely marked that there is no doubt that the three species are all synonymous. It is very evident from the varying determination of duplicate numbers by eminent botanists that the workers were uncertain of these species and have been influenced in naming the specimens by geographical range, material at hand, previous determination and leaf shape.

8a. *Jasminum lanceolarium* Roxburgh var. *puberulum* Hemsley in Jour. Linn. Soc. xxvi. 78 (1889).—Rehder in Sargent, Pl. Wilson. II. 612 (1914).—Chung in Mem. Sci. Soc. China, I. 216 (1924).

Jasminum Dunnianum Léveillé in Fedde, Rep. Spec. Nov. XIII. 151 (1914).—Syn. nov.

H u p e h : ravines, north and south of Ichang, alt. 300–1000 m., *E. H. Wilson*, no. 781A, July and December 1907 (climber 7 m.; flowers white, fragrant) (AA, C); glen near Ichang, *E. H. Wilson*, Veitch Exped. no. 1018, June 1900 (climber with white flowers) (AA); foot of shaded cliff, Liang Sung Gon, alt. 780 m., *W. Y. Chun*, no. 3845, August 10, 1922 (woody vine with leaves light shiny green above, paler beneath) (AA); Ichang, *A. Henry*, nos. 2729, 3669 (G); without precise locality, *A. Henry*, nos. 3000

(AA) and 4562 (G). *Kiangsi*: circa carbonis minas Pinghsiang, alt. 600 m., *Wang Te Hui*, no. 202 in 1920 (flores albi) (AA). *Chekiang*: by the side of an exhausted stream, *Y. L. Keng*, no. 218, July 30, 1926 (trailing plant, woody and pubescent, about 2 m. long) (AA); valley along stream, Sungyang, hsien, alt. 210 m., *H. H. Hu*, no. 426, September 20, 1920 (vine about 3-6 m. with greenish white berries) (AA); on dense bushy slopes, 60 li from Wenchow, *R. C. Ching*, no. 1890 (tough climber; flowers white and scented) (AA). *Fukien*: climbing over thickets in rocky ravine, Buong Kang, Yenping, alt. 700 m., *H. H. Chung*, no. 3585, June 27, 1925 (climber with white scented flowers) (AA, C). *Kwantung*: near Taiping, *W. Y. Chun*, no. 5670, Dec. 11, 1927 (on shrubs in open) (AA); Lok chong, *C. L. Tso*, no. 21001, June 6, 1929 (high climber, twining on trees; flowers white) (NY). *Kweichow*: Che-ten, *J. Esquirol*, no. 887, June 1906 (arbrisseau; fleurs blanches) (AA, type of *J. Dunnianum* Lévl.); inter oppida Kweiting et Tuyün, in silvis umbrosis, faucium prope vicum Madjiaduen, alt. 1100 m., *H. Handel-Mazzetti*, 206 (10649) August 9, 1917 (frutex sarmentosus fl. albis) (AA). *Kwangsi*: in woods, Bin-long, Miu-shan, N. Luchen, alt. 1220 m., *R. C. Ching*, no. 5970, June 14, 1928 (climber 6 m.) (AA).

Jasminum Dunnianum Léveillé is undoubtedly the same as *J. lanceolarium* var. *puberulum*. The variation from the straight species *J. lanceolarium* is only in the character of pubescence and not worthy of specific rank.

9. *Jasminum sinense* Hemsley in Jour. Linn. Soc. Bot. xxvi. 80 (1889).—Diels in Bot. Jahrb. xxix. 533 (1900).—Léveillé, Fl. Kouy-Tchéou, 294 (1914); in Fedde, Rep. Spec. Nov. xiii. 150 (1914).—Rehder in Sargent, Pl. Wilson. ii. 612 (1914).—Chung in Mem. Sci. Soc. China, i. 217 (1924).

Lonicera Rehderi Léveillé in Fedde, Rep. Spec. Nov. x. 145 (1911).—Non Merrill.—Syn. nov.

Lonicera Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. xi. 31 (1912).—Syn. nov.

Jasminum Bodinieri Léveillé in Fedde, Rep. Spec. Nov. xiii. 151 (1914).—Syn. nov.

Hupeh: mountains, Patung, *E. H. Wilson*, Veitch Exped. no. 1576, August 1900 (climber with white flowers) (NY); Nanto and mountains to the northward, *A. Henry*, no. 4464 (G, isotype). *S. W. Hunan*: in ditione oppidi Tsingtschou prope vicum Pukou, in fructicetis, alt. 400 m., *H. Handel-Mazzetti*, no. 336, July 30, 1917 (sarmentosa; fl. albi) (AA). *Fukien*: Hinghwa, *H. H. Chung*, no. 959 in 1923 (AA). *Kwangtung*: Hongkong, *C. Ford* (NY, P); Lin District, *C. O. Levine*, no. 3320, Oct. 14,

1918 (G). *K w a n g s i*: Tsin-hung-shan, N. Hin-yen, alt. 220 m., climbing in thickets, *R. C. Ching*, no. 7023, August 19, 1928 (bark green; flowers white, scented) (AA, NY). *Y u n n a n*: mountains to the north, Mengtze, alt. 1525-1830 m., *A. Henry*, nos. 9657, 9657A, 9657B (climber with white flowers) (AA, NY); Szemao, alt. 1830 m., *A. Henry*, no. 13354 (climber with white flowers) (AA); on trees and scrub, flanks of the Mingkwong valley, lat. 25° 15' N., alt. 2135 m., *G. Forrest*, no. 7861, May 1912 (scandent shrub 2.5-6 m.; flowers interior waxy white, exterior flushed crimson-rose, deliciously fragrant) (AA). *K w e i c h o u*: Pan chouï route de Pin-Fa a Tou-Yun, *J. Cavalerie*, no. 3038, April 9, 1907 (AA, type of *Lonicera Cavaleriei*); environs de Tsin-gay, Gan-pin, *Jean Laborde*, Sept. 1897 (arbuste, sarmenteux; fleurs jaunes (AA, type of *J. Bodinieri* Lévl.). *Western Szechuan*: in thickets, Ya-Chou-Fu alt. 600-900 m., *E. H. Wilson*, no. 2808, August and November, 1908 (climber, 3 m.; flowers white) (AA, G).

There is no doubt but that *Jasminum Bodinieri* Léveillé, *Lonicera Cavaleriei* Léveillé and its synonym *Lonicera Rehderi* Léveillé all belong to *J. sinense*.

Series 3. PINNATIFOLIA DC.

- A. Calyx lobes subulate-setaceous, 5-8 mm. long.
 B. Flowers white.....10. *J. officinale*
 BB. Flowers pink.....11. *J. stephanense*
 AA. Calyx lobes usually obtuse or if subulate not more than 1 mm. long.
 B. Leaflets distinctly trinerved.....12. *J. polyanthum*
 BB. Leaflets five-nerved.....13. *J. dispernum*

10. *Jasminum officinale* Linnaeus, Sp. Pl. i. 7 (1753).—Curtis in Bot. Mag. i. t. 31 (1787).—DeCandolle, Prodr. viii. 313 (1844).—Brandis, Forest Fl. Brit. Ind. 313 (1874); Ind. Trees, 452 (1906).—Boissier, Fl. Or. iv. 43 (1879).—Clarke in Hooker f., Fl. Brit. India, iii. 603 (1882).—Dippel, Handb. Laubholz. i. 150 (1889).—Collett, Fl. Siml. 307 (1902).—Schneider, Ill. Handb. Laubholz. ii. 837, fig. 526 i-m, 527 d-e (1911).—Bailey, Stand. Cyclop. Hort. iii. 1718, figs. 2008 (1915).—Rehder in Sargent, Pl. Wilson. ii. 613 (1916); Man. Cult. Trees Shrubs, 765 (1927).—Chung in Mem. Sci. Soc. China, i. 216 (1924).

Jasminum vulgatum Lamarek, Fl. Franc, ii. 306 (1778).

Jasminum viminalis Salisbury, Prodr. 12 (1796).

Jasminum affine Lindley in Bot. Reg. xxxi. t. 26 (1845).

Y u n n a n: high plateau between Talifu and Likiang to the foot of the Likiang Snow Range, *J. F. Rock*, nos. 3190, 3244 and 3312, May 6-11, 1922 (climber; flowers white with purple tubes) (AA); Pe-long-tsin, alt., 3200 m., *E. E. Maire*, no. 3352 ser. B, June 1910 (fleurs blanches) (NY, P); on scrub on the descent to

the Yangtze, from the eastern boundary of the Lichiang valley, lat. $27^{\circ} 15' N.$, alt. 2740 m., *G. Forrest*, no. 10107, June 1913 (scandent shrub 1.5–4 m.; flowers white, exterior dull rose, fragrant) (AA); in rupibus calcareis, in summa Lan tsching shan, Yunnan fu, alt. 2400 m., *O. Schoch*, no. 206, June 15, 1916 (flores rubicundi) (AA). Szechuan: open rocky, dry situation around Mu-li, lat. $28^{\circ} 12' N.$, long. $100^{\circ} 50' E.$, alt. 2135–2440 m., *G. Forrest*, no. 20417, June 1921 (shrub 0.5–1.0 m.; flowers fragrant, white, flushed purple exterior) (AA); exact locality lacking, ravine, alt. 2740 m. *E. H. Wilson*, Veitch Exped. no. 4074A, June 1904 (flowers white) (AA); Monkong Ting, alt. 2300–2600 m., *E. H. Wilson*, no. 2807, June 1908 (climber 2–3 m., flowers white, fragrant) (AA, G); Te chang, *C. K. Schneider*, no. 702, April 3, 1914 (AA); inter Yenyuan tsien and Hunka, alt. 3800 m., *C. K. Schneider*, no. 1474, June 12, 1914 (flowers white flushed with red) (AA). Southeastern Tibet: on scrub and in thickets in side valleys on the Salween-Kiu-chiang divide, Tsarong, lat. $28^{\circ} 40' N.$, long. $98^{\circ} 15' E.$, alt. 1830–2135 m., *G. Forrest*, no. 19296, August 1919 (scandent shrub 6–9 m., flowers strongly fragrant, white, flushed deep rose exterior) (AA). British India: Langer, Bhandal Valley, Chamba State, alt. 2200 m., *R. N. Parker*, Oct. 2, 1919 (AA); Bhabua village, West Nepal, *Bis Ram*, no. 452, May 21, 1929 (climbing shrub) (AA); Kumaon, *Dr. J. F. Royle*, date and number lacking (G); Panjab, *T. Thomson*, number and date lacking (G); Malabar, Concav, *Stocks, Law and ?* (G).

10a. *Jasminum officinale* Linnaeus forma *grandiflorum* (Linnaeus), comb. nov.

Jasminum grandiflorum Linnaeus, Sp. Pl. ed. 2, i. 9 (1762);—Ker in Bot. Reg. ii. t. 91 (1816).—Roxburgh, Fl. Ind. i. 98 (1820).—DeCandolle, Prodr. viii. 313 (1844).—Wight, Ic. Pl. Ind. Or. iv. t. 1257 (1848).—C. B. Clarke in Hooker f., Fl. Brit. Ind. iii. 603 (1882).—Bailey, Cycl. Am. Hort. ii. 843 (1900); Stand. Cycl. Hort. iii. 1718 (1916).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 150 (1914).—Chung in Mem. Sci. Soc. China, i. 216 (1924).

Jasminum officinale grandiflorum Anon. in V. Lemoine et Fils (Catalogue) no. 173, p. 14 (1909).—nomen nudum.

Yunnan: open moist situation by sides of streams in the Tali Range, lat. $25^{\circ} 40' N.$, alt. 2135–2440 m., *G. Forrest*, no. 4683, May–June 1906 (shrub 2–4 m.; flowers exterior rose, interior white, fragrant) (AA); haies des coteaux derrière Tong-tchouan, alt. 2600 m., *E. E. Maire*, no. 7188 collected in May (grim pant; fleurs blanches) (C); on cliffs, Pu-esh, alt. 1525 m., *A. Henry*, no. 13397 (climber with white flowers) (AA, NY). N. India: Kasmir: Hariwan stream, alt. 1615 m., *G. A. Gamme*, July 10, 1891 (plant 1 m.) (AA); Ganderbal-Kangan, alt. 1830 m., *R. R.*

Stewart, no. 6228, July 14, 1921 (AA); Domel Thelum Valley, alt. 750 m., *Keshavanam*, no. 657, June 1907 (AA). P u n j a b : Taranda, Badhahr State, Simla District, alt. 1800 m., *R. N. Parker*, no. 2979, June 10, 1928 (AA). W e s t e r n H i m a l a y a : Kamálhan, Kagán, *Indyat*, June 17, 1899 (AA); Sultánpur on the Biás River, Prov. Kulu, *Herb. W. J. Hooker*, Cat. no. 12246, June 5, 1856 (G); Kumaon, alt. 1220 m., *R. Strachey and J. E. Witherbottom*, no. 5 (G). B u r m a : Tenasserim and Andamans, *J. W. Helfer*, no. 3718 (G); precise locality lacking, *R. Wight*, no. 1752 (G).

The species *J. officinale* L. and the erstwhile *J. grandiflorum* L. offered considerable difficulty in attempted specific delimitation. No character or group of characters held together consistently enough to permit definite separation. In examining the copious material at hand (both spontaneous and cultivated) it was found that there was a definite gradation in all the diagnostic characters from the larger-flowered forms to the small-flowered specimens; from the longer, lanceolate leaflets to the smaller cuspidate forms; from the long subulate-setaceous calyx teeth to the less conspicuous calyx teeth; in fact, on a single flower cluster were found enough differentiation in calyx teeth length sufficient to be used in specific limitation. However, some specimens, especially those in cultivation presented a larger, more showy flower development. This form is very much cultivated in gardens under the name *J. grandiflorum* and as a result, it seems best, if for this purpose alone, to retain the name *grandiflorum* as a horticultural form of *J. officinale*.

11. \times *Jasminum stephanense* V. Lemoine and Son (Cat.) no. 195, p. 9, pl. (1921).—A. Meunissier in *Rev. Hort.* 1927, p. 643, t.—Mrs. J. N. Henry in *Horticulture*, VIII. 486, fig. (1930). = *J. Beesianum* \times *officinale* f. *grandiflorum*.

Jasminum officinale grandiflorum \times *J. Beesianum* Anon. in *Jour. Soc. Nat. Hort. France*, ser. 4, XXI. 224 (1920).

Y u n n a n : Yangtze watershed, Prefectural District of Likang, eastern slopes of Likang Snow Range, *J. F. Rock*, no. 4509, May–Oct. 1922 (flowers entirely pink) (AA, NY).

This hybrid between *J. officinale grandiflorum* and *J. Beesianum*. was first exhibited as an artificial hybrid by M. Thomas Javit at the Flower Show of the Société Nationale d' Horticulture de France in July 1920. Until recently it had not been known as a natural hybrid. However, it is interesting to know that this beautiful hybrid Jasmine combining the attractive coloring of *J. Beesianum* with the fragrance of its other parent was collected by Rock in Yunnan almost at the same time of its presentation to the public in artificial form. Besides the spontaneous specimen of J. F. Rock,

material collected from a plant given the Arboretum by Mrs. J. N. Henry of Gladwyne, Pa., was obtainable also. Mrs. Henry says that the plant grows luxuriously at both her Pennsylvania and Maryland homes. Unfortunately it is not hardy as far north as Massachusetts. An excellent flowering specimen collected at the Vilmorin Nurseries at Verrières is in the herbarium of the Arnold Arboretum.

The name *stephanense* refers to Saint-Etienne, the place where the hybridization was made; Stephanus being the latin equivalent of Etienne.

12. *Jasminum polyanthum* Franchet in Rev. Hort. 1891, p. 270, fig. 69; Léveillé in Fedde, Rep. Spec. Nov. XIII. 150 (1914).—Chung in Mem. Sci. Soc. China, I. 216 (1924).

Jasminum Blinii Léveillé in Fedde, Rep. Spec. Nov. XIII. 151 (1914);

Cat. Pl. Yun-nan 179 (1916).—*Syn. nov.*

Jasminum Delafieldii Léveillé, Cat. Pl. Yunnan 179 (1916).—*Syn. nov.*

Y u n n a n : Mengtze, alt. 1525 m., *A. Henry*, no. 10314 (AA); Chu-yuan, *A. Henry*, no. 10314A (AA); Kon ya hua, Mengtze woods, alt. 1400 m., *A. Henry*, no. 10314B ("dog's tooth flower"; large climber; flowers with white lobes and pink corolla tubes; strong odor, worn by women for adorning the hair) (AA, NY); mountain forests, Szemao, alt. 1525 m., *A. Henry*, no. 11656 (climber with white flowers) (AA); in collibus calcareis, Yunnan fu, alt. 2000–2200 m., *O. Schoch*, no. 18, April 24, 1916 (frutex valde scandens) (AA); amongst scrub in the Tali valley and along the base of the eastern flank of the Tali Range, lat. 25° 40' N., alt. 2040–2440 m., *G. Forrest*, no. 4658, May–August 1906 (weakly scandent shrub 2–3 m.; flowers, interior white, exterior rose, strongly fragrant) (AA); on scrub in open situations, hills around Tengyueh, lat. 25° N., alt. 1675–2135 m., *G. Forrest*, no. 9761, March 1913 (scandent shrub 2–6 m.; flowers, interior white, exterior red) (AA); haies de Tso-si, alt. 2900 m., *E. E. Maire* (AA no. 253) April 19—(arbuste grimpant à longs rameaux toujours verts; fls. branches levées de rose) (AA); Yunnan-fu, alt. 2200 m., *Harry Smith*, no. 1622, Sept. 4, 1922 (flores rosei) (AA); haies de Ma-Tchang près Tchen-Lin, *J. Esquirol*, April 28, 1906 (très belle fleur pendant en longs festons, rosée à l'intérieur) (fragment and photo of type of *J. Delafieldii* in AA, type at E); precise locality lacking, *F. Ducloux*, nos. 58, 800 (NY). K w e i c h o u : Gan-chouen, *J. Cavalerie*, no. 3912, May 1912 (liane; fleurs blanches) (AA, G) (iso-syntypes of *J. Blinii*).

The two species *Jasminum Blinii* and *J. Delafieldii* described by Léveillé are found on careful study to be conspecific with *J. polyanthum* Franchet.

13. *Jasminum dispernum* Wallich in Roxb. Fl. Ind. ed. Carey, I. 99 (1820); Pl. As. Rar. III. t. 274 (1832).—D. Don, Prodr. Fl. Nepal. 106 (1825).—DeCandolle, Prodr. VIII. 310 (1844).—Brandis, For. Fl. Brit. Ind. 313 (1874).—C. B. Clarke in Hooker f., Fl. Brit. Ind. III. 602 (1882).—Duthie, Fl. Upper Gangetic Plain, II 23 (1911).—C. J. Bamber, Pl. Punjab, 588 (1916).—Parker, For. Fl. Punjab, Hazara and Delhi, ed. 2, 320 (1924).—Ostweston, For. Fl. Kumaon, 335 (1927).

Jasminum quinquerive Lambert ex D. Don, Prodr. Fl. Nepal. 106 (1825).

Y u n n a n : watershed of the Black River or Papienho, between Mohei and Maokai beyond Chugai, alt. 2040 m., *J. F. Rock*, no. 3016, April 7, 1922 (scandent shrub, 3–4.5 m.; flowers white inside, purplish red outside; drupes blackish blue) (AA); on the Shweli-Salween divide, lat. 25° 30' N., alt. 2040 m., *G. Forrest*, no. 15720, July 1917 (AA). British India: Sanpra, West Nepal, *Bis Ram*, no. 460, May 23, 1929 (climber) (AA); Katai, West Nepal, *Bis Ram*, no. 124, Mar. 28, 1929 (AA); Camp Dharamsala, Distr. Kangra Punjab, *Bis Ram*, no. 326, June 6, 1928 (AA); Sikkim, alt. 1500 m., *G. King*, Feb. 19 and March 24, 1876 (AA); Sikkim, alt. 1500–1560 m., *J. D. Hooker* (G); Himalaya bor. occidentalis, alt. 1800–2400 m., *T. Thomson* (G); in hedges on road from Chuari to Sihunta, Bhatiyat Wagirat, Chamba State, alt. 900–1050 m., *R. N. Parker*, Oct. 1, 1920 (AA); Konoma, Assam, alt. 1500 m., *Dr. King's Collector*, no. 220, April 1896 (AA); Lyndoh Forest, Mawphlang, K. and J. Hills, Assam, alt. 1800 m., *Upen-dranath Kanjilal*, no. 4656, Oct. 22, 1914 (AA); Kumaon, alt. 2100 m., *R. Strachey and J. E. Winterbottom*, no. 6 (G); Mussoonia, Siwalik and Jaunsar Divisions, Chandan, *Singh Rawat* no. 76, June 9, 1921 (scandent shrub) (AA).

Series 4. UNIFOLIOLATA DC.

- A. Calyx lobes diminutive, obtuse, not subulate-setaceous.
- B. Corolla 35 mm. (in toto); tube 25 mm. long; leaf 18 cm. long, 8 cm. wide.....14. *J. coffeinum*
- BB. Corolla about 25 mm. long or less; leaves hardly ever over 4 cm. wide, usually considerable less.
- C. Inflorescence terminal, a many-flowered, diffuse cyme, up to 10 cm. wide, corolla tube and lobes (linear) nearly equal.
15. *J. Seguinii*
- CC. Inflorescence terminal and axillary, usually in close clusters, corolla tube considerably longer than lobes (acute).
- D. Leaves usually 9–16 cm. long, 3–4 cm. wide, lanceolate or oblong lanceolate; Western China (Yunnan).
16. *J. dumicolum*
- DD. Leaves 3.5–8.5 cm. long, 1.5–4 cm. wide, ovate; Eastern China (Kwantung).....17. *J. microcalyx*

AA. Calyx lobes subulate-setaceous.

B. Calyx glabrous.

C. Leaves coriaceous or sub-coriaceous.

D. Fruit yellow; leaves lanceolate.....18. *J. Prainii*

DD. Fruit black; leaves ovate.....19. *J. pentaneurum*

CC. Leaves not coriaceous.

D. Flowers red; fruit yellow.....20. *J. Beesianum*

DD. Flowers white; fruit black.....21. *J. anastomosans*

BB. Calyx pubescent.

C. Leaves and branchlets flavescent; leaves 2-4 cm. long, chartaceous.

22. *J. nintoooides*

CC. Leaves glabrous or pubescent, not flavescent, seldom less than 6 cm. long.

D. Leaves very thin, membranaceous, reticulations outstanding on upper surface and lower surface; flowers double.

23. *J. sambac*

DD. Leaves not particularly thin, some near coriaceous, upper surface not noticeably reticulate.

E. Stem leaves cordate at base.....24. *J. multiflorum*

EE. Stem leaves cuneate or truncate at base.

F. Leaves distinctly cuneate at base.....25. *J. coarctatum*

FF. Leaves truncate, or nearly so at base; not cuneate.

26. *J. amplexicaule*

14. *Jasminum coffeinum* Handel-Mazzetti in Anz. Akad. Wiss. Wien, LXII. 235 (Pl. Nov. Sin. Forts. 37; p. 2) (1925).

Yunnan: In bambusetis et silvis apertis tropicis ex adverso supra vicum Manhao prope fines Tonkinensis, substr. schisto argilloso, alt. 200 m., *H. Handel-Mazzetti*, no. 5827, March 1, 1915 (flores albi extus rubri) (isotype in AA).

15. *Jasminum Seguinii* Léveillé in Fedde, Rep. Spec. Nov. XIII. 151 (1914).

Jasminum taliense, W. W. Smith in Notes Bot. Gard. Edinb. XII. 210 (1920).—*Syn. nov.*

K w e i c h o u : Rochers de la cascade aux environs de Hoang-Ko-Tchou, *J. Seguin*, in herb. E. Bodinier, no. 2354 June 9, 1898 (arbuste liane; fleurs blanches) (isotype in AA). Y u n n a n : on scrub and trees, western flank of the Tali Range, lat. 25° 40' N., alt. 3050 m., *G. Forrest*, no. 11667, Aug. 1913 (scandent shrub 2-3 m.; flowers fragrant, interior creamy white, exterior flushed crimson) (isotype of *J. taliense* in AA, C); amongst scrub, western flank of the Tali Range, lat. 25° 40' N., alt. 2740 m., *G. Forrest*, no. 15605, July 1917 (semi-scandent shrub 2-3 m.; flowers white with flushed rose exterior, fragrant) (isotype of *J. taliense* in AA); on scrub in thickets on the N'Maikha-Salwin divide, lat. 26° 20' N., alt. 2740 m., *G. Forrest*, no. 18330, August 1919 (scandent shrub 3-3.5 m.; flowers white, exterior, faintly flushed rose fragrant) (AA); in thickets by streams in side valleys on the Chien-chuan-Mekong divide, lat. 26° 30' N., long. 99° 40' E., alt. 2135-

2440 m., *G. Forrest*, no. 23166, July 1922 (scandent shrub 2-6 m.; flowers white with flushed purple-rose exterior, fragrant) (AA); south forests, Szemao, alt. 1525 m., *A. Henry*, nos. 12661 and 12661A (large climber with white flowers) (AA, NY); in valle fluminis Yangtze, prope Ta ku, alt. 2500 m., *C. K. Schneider*, no. 2150, August 1914 (fl. albo-flavi) (AA); ex colle Tong chan, Tie So, *Simeon Tén*, no. 131, May 30, 1916 (frutex prostrata ad 1 m.; floribus albi) (AA); Yangpi road in mountains of the Yangpi river drainage basin, *J. F. Rock*, no. 6214, August 1922 (flowers white, fragrant) (AA); Mengtze, *A. Henry*, nos. 9581, 9581B, 9581c (climbing shrub 1-1.5 m.; flowers white; fruit black) (AA, NY); dry forest edge of paddy plain, Muang Hun, *J. F. Rock*, no. 2440, Feb. 14, 1922 (woody vine with scandent branches) (AA). Sze ch u a n : inter pagum Telipu et flumen Yalung, alt. 2000 m., *C. K. Schneider*, no. 1137, May 5, 1914 (frutex sub-scandens; fl. albi, valde odorati) (AA).

There seem to be no difference between the two types to warrant specific delimitation.

16. *Jasminum dumicolum* W. W. Smith in Notes. Bot. Gard. Edinb. XII. 207 (1920).

Jasminum Schneideri Léveillé, in herb.

Y u n n a n : among scrub, Shweli Valley, lat. 25° N., alt. 1525-1830 m., *G. Forrest*, no. 7926, May 1912 (shrub 2-3 m.) (isotype in AA); on scrub and trees, hills to the east of Tengyueh, lat. 25° N., alt. 1830-2135 m., *G. Forrest*, no. 8094 (scandent shrub 2-3 m.) (isotype in AA); on trees and scrub in rather shady situations, western flank of the Shweli-Salween divide, lat. 25° 10' N., alt. 2440-2740 m., *G. Forest*, no. 9346, Dec. 1912 (scandent shrub 3-5 m.; flowers exterior deep crimson rose, interior white or flushed rose, fragrant) (isotype in AA); on trees, Ma-chang-kai Valley, north of Tengyueh, lat. 25° 20' N., alt. 1830 m., *G. Forrest*, no. 9531, Feb. 1913 (scandent shrub 6-9 m.; flowers interior white, exterior dull rose, fragrant) (isotype in AA); on scrub, Ma-chang-kai Valley, lat. 25° 20' N., alt. 1830-2135 m., *G. Forrest*, no. 9757, March 1913 (scandent shrub 2-3.5 m.; flowers interior creamy white, exterior deep dull crimson) (isotype in AA); mountain forests, Mengtze, alt. 1525 m., *A. Henry*, no. 10634A (large climber) (isotype in NY); Szemao, *A. Henry* 11708 (large climber) (NY); at Kao shan ssu, Shweli River drainage basin to summit of Shweli-Salween watershed, east of Tengyueh, *J. F. Rock*, no. 7894, Nov. 1922-March 1923 (climber; flowers white inside, purplish outside, fragrant) (AA); environs de Mý tsaô, *F. Ducloux*, no. 112, March 4, 1897 (tiges s'enlaçant aux arbores et buissons; fleurs blanches,

boutons roses) (AA; photo. and fragments of type of *J. Schneideri* Lévl. from E).

17. *Jasminum microcalyx* Hance in Jour. Bot. xxi. 323 (1883).—Hemsley in Jour. Linn. Soc. London, xxvi. 79 (1889).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 149 (1914).—Chung in Mem. Sci. Soc. China, i. 216 (1924).—Merrill in Lingnan Sci. Jour. V. 147 (1927).

Jasminum inornatum Hemsley in Jour. Linn. Soc. xxvi. 78 (1889).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 149 (1914).—Chung in Mem. Sci. Soc. China, i. 216 (1924).—Syn. nov.

H a i n a n : Hoi-hau, *B. C. Henry*, no. 22171 (Hance Herb.) Oct. 19, 1882 (type; photo. in AA, carbon tracing in NY); in dry thickets, Hoi-hau, *F. A. McClure*, no. 7595, Oct. 10, 1921 (bushy vine with fragrant, white flowers) (NY). K w a n t u n g : without precise locality, *C. Ford*, no. 113 (type; photo. in AA, carbon tracing in NY).

Although little known, the species *J. microcalyx* is quite outstanding in its nearly obsolete calyx-lobes. Hemsley's *J. inornatus* described six years later is conspecific with *J. microcalyx*.

18. *Jasminum Prainii* Léveillé in Fedde, Rep. Spec. Nov. x. 148 (1911); xiii. 151 (1914).

K w e i c h o u : route de Pin-fa ad Ou-glan *J. Cavalerie*, August 1908 (E, type; AA, isotype).

There is a superficial resemblance between *J. Prainii* Léveillé and *J. dumicolum* W. W. Smith. However, *J. dumicolum* possesses calyx-lobes of a more obtuse nature while *J. Prainii* has calyx lobes distinctly subulate-setaceous.

19. *Jasminum pentaneurum* Handel-Mazzetti in Anz. Akad. Wiss. Wien, LIX. 110 (Pl. Nov. Sin. Forts. 16, p. 9) (1922).

K w a n t u n g : In monte Dingwu-schan ad occid. urbis Kanton, *R. Mell*, no. 215 March 26, 1918 (photo. of type in AA); in montibus Lungtou-schan loco Siuhang dicto, alt. 300 m., *R. Mell*, no. 922, Nov. 18, 1917 (fragment of type in AA); Loting, *Y. Tsiang*, no. 1143, Sept. 14, 1928 (AA, NY); on side of river, Ting Wu Shan, *Y. Tsiang*, no. 1490, Nov. 5, 1928 (scandent) (AA, NY); in dense mixed woods, Kochow District, *Y. Tsiang* no. 2244A, May 11, 1929 (AA); Tseh Tse Dee, West River, Yun Fou district, *Y. K. Wang*, no. 321, Jan. 14, 1928 (AA); on roadside, Yun Fou District, *Y. K. Wang*, no. 1832, Feb. 12, 1929 (NY); in mixed woods, Ting Wu Shan, *W. Y. Chun*, no. 6344, May 5, 1928 (scandent) (AA); in valley, Tsing Yun District, *W. Y. Chun*, no. 30472, March 23, 1930 (suffruticose) (NY); scattered along trail near stream above

monastery, Ting Woo Mts., alt. 300 m., *C. O. Levine*, no. 2016, May 26, 1918 (C); Poon Yue District, *Ah To*, Hb. no. 3177, Oct. 30, 1918 (flowers white) (C); same locality, *C. O. Levine*, Hb. no. 3180, Nov. 1, 1918 (AA); Ting Woo Mt., *C. O. Levine & G. W. Goff*, no. 42, Nov. 18, 1916 (AA); in woods, Teng wu shan, *H. T. Ho*, no. 60041 (shrub) (NY); exact data lacking, *G. Ford*, (NY). *K w a n g s i*: Bako-shan, W. Poseh, alt. 900 m., *R. C. Ching*, no. 7521, Sept. 18, 1928 (tough straggling climber on trees, 9 m.; flowers white, star shaped) (AA).

This recently described species although quite outstanding and frequently collected especially in Kwangtung has been usually identified with *J. laurifolium* Roxb., *J. subtripinerve* Bl. and *J. nervosum* Lour. The two former species are probably confined to the Himalayan region only, while the latter, *J. nervosum* Lour. seems to be of rather dubious status and closely allied to *J. anastomosans*. This would seem to account for the seeming confusion.

20. *Jasminum Beesianum* Forrest & Diels in Notes Bot. Gard. Edinb. v. 253 (1912).—Léveillé, Fl. Kouy-Tchéou, 293 (1914); in Fedde, Rep. Spec. Nov. XIII. 149 (1914).—Rehder in Sargent, Pl. Wilson. II. 615 (1916).—Chung in Mem. Sci. Soc. China, I. 216 (1924).

Jasminum Wardii Adamson in Jour. Bot. LI. 131 (1913).—Syn. nov.

Jasminum Delavayi Franchet ex Diels in Notes Bot. Gard. Edinb. v. 253 (1912), in obs.

Jasminum Valbrayi Léveillé in Fedde, Rep. Spec. Nov. XIII. 337 (1914).

—Syn. nov.

Jasminum violascens Lingelsheim in Fedde, Rep. Spec. Nov. Beih. (Limpricht, Bot. Reise Hochgebirg. China & Ost-Tibet) XII. 463 (1922).—Syn. nov.

Y u n n a n: amongst rocks and stone on dry, barren, open ground at south end of the Sung-kwei valley, lat. 26° 20' N., alt. 2440–2740 m., *G. Forrest*, no. 2021, April 1906 (shrub to 1 m.; flowers pink or deep rose, strongly fragrant) (AA, isotype); Lichiang Range, lat. 27° 15' N., alt. 2740–3200 m., *G. Forrest*, no. 10066, June 1913 (AA); around Pe Yen Tsin (Tong-tschoun) *Simeon Tén*, no. 499, April 5, 1919 (prostrate shrub with red flowers) (AA); in dumetis ad vicum Djuandjiadio et Tschapoling prope oppidum Sidsung, alt. 1900–2000 m., *H. Handel-Mazzetti*, no. 20, June 9, 1917 (fruticulus subscandens: fl. intense rosei) (AA); ad pedem montium niveosorum prope Lichiang in dumetis ad rivulos, alt. 2900 m., *C. K. Schneider*, no. 3199, Oct. 1914 (AA); in regione Lichiang prope pagum Ngu Leh keh, alt. 2900 m., *C. K. Schneider*, no. 2082, July 31, 1914 (scandens) (AA); climbing over Roses on high plateau between Talifu and Likiang to the foot of the Likiang Snow Range, *J. F. Rock*, no. 3216, May 6–11,

1922 (AA, NY); in summa montis Mangan in rupibus calc., alt. 2400 m., *O. Schoch*, no. 207, May 26, 1916 (AA); haies-plaine de Tong tchouan, alt. 2500 m., *E. E. Maire* (AA no. 108) (arbrisseau grimpant toujours; fl. carmine) (AA); haies de la plaine à Tong-tchouan, alt. 2500 m., *E. E. Maire*, no. 3310, May 1911 (fl. rouge pourpre) (NY, C); haies, plaine de Tong-tchouan, alt. 2500 m., *E. E. Maire*, May 1913 (fleurs d'un rouge carmin) (AA, isotype of *J. Valbrayi*); precise data lacking, *E. E. Maire*, no. 7417 (NY); precise data lacking, *F. Ducloux*, no. 6 (K) and no. 483 (AA). *Szechuan*: in prato herboso, Teng-ksiang-ying, alt. 2100 m., *Harry Smith*, no. 1886, May 20, 1922 (frutex humilis ad 3 dm. altus; flor. roseis-rubris) (AA); near Si tchi, Ning yuan fu, *C. K. Schneider*, no. 905, April 15, 1914 (AA); Lololand, östlich von Chao kio bei heisser Quelle, *C. K. Schneider*, no. 973, April 23, 1914 (AA); precise locality lacking, ravine, alt. 900–1830 m., *E. H. Wilson*, Veitch Exped. no. 4074, June 1904 (climber with rose flowers) (AA). *East Tibet*: Dawo, Tal von Lumpu, alt. 3900 m., *Dr. Wolfgang Limpricht*, no. 2006, July 15, 1914 (AA, photo. of type of *J. violascens* deposited at Herb. Breslau).

Jasminum Beesianum Forrest & Diels is probably one of the most outstanding species in the genus. Its distinctly ovate, attenuate leaves and its red flowers make it noticeably different. Adamson in describing *J. Wardii* was just one year later than Forrest and Diels in publishing his description of the species. Although not having seen the type of *J. Wardii*, another specimen collected by F. Ducloux and mentioned in the description by Adamson was loaned us by Kew and proves to be identical with *J. Beesianum*.

J. Delavayi Franchet as stated by Diels in an explanatory paragraph supplementing the original description of *J. Beesianum* is merely a name on a specimen in the Paris Herbarium collected by Bonvalot and the Prince of Orléans, between Batang and Litang in a humid valley on June 19th.

Photographs of the types of *J. Valbrayi* Léveillé and *J. violascens* Lingelsheim are in Arnold Arboretum herbarium. All these names mentioned above are clearly synonyms of *J. Beesianum*.

21. *Jasminum anastomosans* Wallich, Cat. 2863 (1829), nomen nud.—Kurz, For. Fl. Brit. Burma, II. 152 (1877).—DeCandolle, Prodr. VIII. 305 (1844).—C. B. Clarke in Hooker f., Fl. Brit. Ind. III. 596 (1882).—Léveillé in Fedde, Rep. Spec. Nov. XIII. 149 (1914).—Chung in Mem. Sci. Soc. China, I. 216 (1924).

? *J. nervosum* Loureiro, Fl. Cochinch. I. 20 (1793).

Yunnan: Szemao, alt. 1370 m., *A. Henry*, no. 11969, April

26 (climber on shrubs; white flowers) (AA, NY); between Keng Hung and Muang Hing, above Pang Khun, alt. 1380 m., *J. F. Rock*, no. 2611, Feb. 26, 1922 (twiner among tree branches) (AA); dry jungle, plain of the Keng Hung, alt. 750 m., *J. F. Rock*, no. 2507, Feb. 17, 1922 (stems dark green with a blackish tinge; petals pinkish) (AA). *K w a n g s i*: in bush, I-shan, alt. 210 m., *R. C. Ching*, no. 5175, May 22, 1928 (AA). *K w a n t u n g*: on open, extensive plain, Pon-tan, Luichow, alt. 210 m., *Y. Tsiang*, no. 2544, June 2, 1929 (scandent vine with white flowers) (AA, NY); on shrub in village common and roadside, Hainan, *F. A. McClure*, no. 9193, April 20, 1922 (vine 2-4 m.; flowers white, fragrant; fruits purple, black when ripe) (AA); Hainan, *A. Henry*, no. 8456, Nov. 1889 (G); Hainan, *Katsumatra* (Hongkong Herb. no. 5406) (C); in dense mixed woods, Koliangling, Kochow, alt. 255 m., *Y. Tsiang*, no. 2221, May 10, 1929 (scandent vine) (NY); same locality, *Y. Tsiang*, no. 2244, May 11, 1929 (scandent vine) (NY).

The synonymy of this species is rather difficult to express because of the fact that *J. anastomosans* has usually been considered a Himalayan rather than a Chinese species. C. B. Clarke in Hooker's *Flora of British India* lists *J. stenopetalum* Lindley, *J. trinerve* Roxburgh and *J. laurifolium* Wallich, non Roxburgh, as synonyms of *J. anastomosans*. Although these last named may be true synonyms of *J. anastomosans* they have not been treated as such in this paper because none of the type specimens or, in fact, any specimens bearing these determinations have been seen by the author.

J. nervosum Loureiro which is questionably cited under this species has heretofore been considered a good Chinese species. However, in examining the material so labeled one finds that the majority of specimens belong to *J. pentaneurum* Hand.-Mazz. leaving only a few sheets to this species. The original description is rather confusing and probably the cause of most of the misunderstanding because it is quite impossible to understand from it just what Loureiro intended as *J. nervosum*. He refers to the leaves as "folia impari pinnata." This, of course, would eliminate *J. nervosum* from the section Unifoliolata unless the small lateral branches were here mistaken for compound leaves. In this case, his description would read folia pari pinnati because of the terminal pair of leaflets. No type or authentic material seems to be available so *J. nervosum* is best treated here as a dubious synonym of its most closely allied species.

Confused with this same group of specimens was the Himalayan

species *J. laurifolium* Roxburgh. A single specimen collected by one of Dr. Prains' collectors, no. 885 made in the jungle near Naga Hill in Assam in April 1899 answers the original description made by Roxburgh and agrees well with an illustration in Botanical Register VII. t. 521 (1821). *Jasminum laurifolium* probably is then distinctly a Himalayan species and one not to have more than a nominal inclusion here.

Léveillé described in Fedde, Rep. Spec. Nov. XIII. 151 (1914) a new variety, *J. laurifolium* Roxb. var. *villosum*. This is probably a variety of *J. anastomosans*. Undoubtedly he was working with material of *J. anastomosans* incorrectly labeled *J. laurifolium* and had this in mind when he described his new variety. A very fragmentary specimen (in fact, only a leaf and a single flower) of the type is at present in the herbarium of the Arnold Arboretum. It seems to agree with *J. anastomosans* in all respects save its pubescent character. However, although there is quite a positive feeling that the material is a variation of *J. anastomosans* one hardly feels justified in making the actual variety transfer on such sparse evidence.

22. *Jasminum nintoooides* Rehder in Sargent, Pl. Wilson. II. 615, 1916.—Chung in Mem. Sci. Soc. China, I. 216 (1924).

Y u n n a n : trailing and climbing over rocks, Mengtsze, alt. 1600 m., *A. Henry*, nos. 9433, type (AA, NY) and 9433A, 9433B (flowers white) (AA).

23. *Jasminum sambac* (L.) Aiton, Hort. Kew. I. 8 (1789).—Willdenow, Sp. Pl. I. 35 (1797).—Edwards in Bot. Reg. I. 1 (1815).—Wallich, Cat. n. 2868 (1829).—DeCandolle, Prodr. VIII. 301 (1844).—C. B. Clarke in Hooker f., Fl. Brit. Ind. III. 591 (1882).—Hemsley in Jour. Linn. Soc. XXVI. 80 (1889).—Bailey, Cycl. Am. Hort. II. 843 (1900); Stand. Cycl. Hort. III. 1717 (1915).—Léveillé in Fedde, Rep. Spec. Nov. XIII. 149 (1914).—Chung in Mem. Sci. Soc. China, I. 216 (1924).

Nyctanthes Sambac Linnaeus, Sp. Pl. I. 6 (1753).

Nyctanthes undulatum Linnaeus, Sp. Pl. I. 6 (1753).

Jasminum bicorollatum Noronha in Verh. Batav. Gen. v. ed. 1, art. IV. 19 (1790).

Jasminum odoratum Noronha in Verh. Batav. Gen. v. ed. 1, art. IV. 19 (1790).

Mogorium Sambac Lamarck, Encycl. Méth. IV. 210 (1796); Ill. I. t. 6, fig. 1 (1823).

Mogorium undulatum Lamarck, Encycl. Méth. IV. 212 (1796).

Jasminum fragrans Salisbury, Prodr. 12 (1796).

Jasminum Zambac Roxburgh, Hort. Beng. 3 (1814), nomen; Fl. Ind. I. 87 (1820).

Jasminum pubescens Buchanan-Hamilton ex Wallich, Cat. sub no. 2880 (1829), nomen.—Jackson, Ind. Kew. I. 1250 (1893), as syn. of *J. sambac*.

Jasminum quadrifolium Buchanan-Hamilton ex Wallich, Cat. no. 2868 (1829), nomen.—Jackson, Ind. Kew. i. 1250 (1893), as syn. of *J. sambac*.

Jasminum quinquesflorum Heyne ex Wallich, Cat. no. 2878 (1829), nomen.—Jackson, Ind. Kew. i. 1250 (1893), as syn. of *J. sambac*.

Jasminum undulatum Hort. Heyne ex Wallich, Cat. No. 2871 (1829), nomen.—Jackson, Ind. Kew. i. 1251 (1893), as syn. of *J. sambac*.

Jasminum Heyneanum Wallich, Cat. no. 2871 (1829), nomen.—Jackson, Ind. Kew. i. 1250 (1893), as syn. of *J. sambac*.

Jasminum sambuc Wight, Ic. II. t. 704 (1843).

K w a n g s i : Moo-shan, Luchen, alt. 540 m., *R. C. Ching*, no. 5394, May 26, 1928 (climber 2.5 m.; flowers white, scented) (AA).

K w a n g t u n g : Honam Island, *C. O. Levine* no. 910, June 18, 1917 (AA). **F u k i e n** : dry place on Ling Pu Mt., vicinity of Foochow, *Tang Siu Ging* (under direction of F. P. Metcalf), no. 5196, Oct. 26, 1926 (AA); Foochow, *H. H. Chung*, no. 3836, Aug. 27, 1925 (shrub 0.70 m. tall; flowers white) (AA).

This species has been so long in cultivation that it is now quite difficult to cite its original spontaneous source with certainty. It is commonly known as the Arabian Jasmine. However, it is so commonly cultivated in China that one feels all the specimens cited are cultivated (even though no mention is made on the label) or escaped from cultivation.

The synonyms of such a popular species are many but the species itself is so distinct that, as a rule, the synonyms can be easily recognized as such. An interesting exception is *Jasminum Blancoi* Hasskarl (Flora, XLVII. 4, 1864) cited by Merrill in Enum. Philipp. Flow. Pl. II. 308 (1923) as a synonym of *J. sambac*. It seems Merrill overlooked the fact that Hasskarl mentions *Nyctanthes Sambac* Blanco, non L., as a synonym to his species. Hasskarl says that the leaves are compound and that there is a relationship between *J. Blancoi* and *J. grandiflorum* L. Blanco in describing *Nyctanthes Sambac* Blanco in Fl. Filip. 9 (1837) calls the leaves compound and mentions three pairs of leaflets. Of course, he had something entirely different from *Jasminum sambac* (L.) Aiton in mind.

This is probably only an oversight on the part of Dr. Merrill because his identified specimens of *J. sambac* from the Philippine Islands accord with *J. sambac* from China and India, as we interpret it, by having simple, opposite leaves.

24. *Jasminum multiflorum* (Burman f.) Andrews, Bot. Repos. VIII. t. 496 (1807).—Heyne apud Roth, Nov. Pl. Sp. 6 (1821).—Merrill, Fl. Manila, 366 (1912); Enum. Philipp. Flow. Pl. III. 307 (1923).

Nyctanthes multiflora Burman f., Fl. Ind. 5. t. 3, f. 1 (1768).

Nyctanthes pubescens Retzius, Obs. v. 9 (1789).

Jasminum pubescens Willdenow, Sp. Pl. i. 37 (1797).—Roxburgh, Fl. Ind. i. 90 (1820).—DeCandolle, Prodr. viii. 302 (1844).—C. B. Clarke in Hooker f., Fl. Brit. Ind. iii. 592 (1882).—Hemsley in Jour. Linn. Soc. xxvi. 80 (1889).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 149 (1914).—Chung in Mem. Sci. Soc. China, i. 216 (1924).

Mogorium pubescens Lamarck, Encycl. Méth. iv. 213 (1797).

Jasminum Esquirolii Léveillé in Fedde Rep. Spec. Nov. x. 147 (1911).—Syn. nov.

K w a n g s i : Hin Yen, R. C. Ching, no. 6667, August 4, 1928 (AA). K w a n t u n g : Canton, Central Park, Y. Tsiang, no. 1574, Nov. 28, 1929 (AA, NY); probably on Canton Christian College Campus, Canton, G. W. Groff, Herb. no. 11501, date lacking (C). K w e i c h o w : Hang-Tong, J. Esquirol, no. 729, June 1906 (arbrisseau; fleurs blanches) (AA, isotype of *J. Esquirolii*).

In all three treatments of the Chinese Jasminums the authors have treated this species under the name *J. pubescens* Willd. This name was based on a transfer to the genus *Jasminum* of a species named *Nyctanthus pubescens* Retzius described in 1789. However, Burman f. in 1768 (twenty-one years earlier) described *Nyctanthes multiflorum* which is synonymous. Andrews made the transfer of *Nyctanthes multiflora* to *Jasminum multiflorum* in 1807. However, with the exception of Heyne (apud Roth) in 1821 and later Merrill in 1912 and 1923, the synonym *J. pubescens* Willd. was used universally in botanical literature.

Léveillé's *Jasminum Esquirolii* described in 1911 is also a synonym according to the isotype in this herbarium.

25. *Jasminum coarctatum* Roxburgh, Fl. Ind. i. 91 (1820).—DeCandolle, Prodr. viii. 308 (1844).—Chung in Mem. Sci. Soc. China, i. 216 (1924).

Jasminum reticulatum Wallich, Cat. no. 2869 (1829), nomen.—De Candolle, Prodr. viii. 303 (1844).

Y u n n a n : South Road, Szemao, alt. 1525 m., A. Henry, nos. 11653 and 11653A (climber with white flowers) (AA, NY); Red River Valley near Manpan, alt. 900 m., A. Henry, no. 10887 (shrub 3 m. with white flowers) (AA); near Muang Hun plain, between Muang Hun and Muang Hai, alt. 1290 m., J. F. Rock, no. 2416, Feb. 13, 1922 (AA); climber on ridge near Szemao, between Muang Hing and Szemao and the Szemao hills proper, alt. 1650 m., J. F. Rock, no. 2763, March 3, 1922 (AA); same locality, J. F. Rock, no. 2781, March 9, 1922 (AA). A s s a m : precise locality lacking, Colonel F. Jenkins (G).

26. *Jasminum amplexicaule* Buchanan-Hamilton in Wallich, Cat. no. 2853 (1829), nomen.—G. Don, Gen. Syst. iv. 60 (1837).—DeCandolle, Prodr. viii. 306 (1844).

Jasminum undulatum Ker-Gawler in Bot. Reg. vi. t. 436 (1820).—Savi, Fl. Ital. iii. t. 85 (1824).—C. B. Clarke in Hooker f., Fl. Brit. Ind. iii. 592 (1882).—Hemsley in Jour. Linn. Soc. xxvi. 81 (1889).—Léveillé in Fedde, Rep. Spec. Nov. xiii. 149 (1914).—Chung in Mem. Sci. Soc. China, i. 217 (1924).—Non Willd.

Jasminum aristatum Wallich, Cat. no. 2875 (1829), nomen.—DeCandolle, Prodr. viii. 314 (1844).

Jasminum scandens Griffith, Itin. Notes, 102 (1848).—Non Vahl.

K w a n t u n g : Hainan, C. Ford, May 19, 1893 (AA, NY); roadside Hainan, near Kingchow, F. A. McClure, 2353, April 5, 1922 (vine 7 m. high, with very fragrant white flowers) (C); Hwa Die, Canton, Y. Tsiang, no. 417, May 25, 1928 (AA); in open field on way to Hwang-lung-kwan, Lonfoushan Mts., East River Region, alt. 232 m., Y. Tsiang, no. 1615, Dec. 18, 1928 (scandent shrub with white flowers) (AA); in dense mixed woods, Vutzeling, Kochow, alt. 830 m., Y. Tsiang, no. 2292, May 14, 1929 (scandent shrub; leaves lustrous green above, lighter below; fruit very young greenish) (AA, NY); in open places, North Gate, Kochow, Y. Tsiang, no. 2437, May 23, 1929 (shrub with white flowers) (NY); in open places along side of West Lake, Liuchow, Y. Tsiang, no. 2573, June 3, 1929 (scandent shrub with white flowers) (AA, NY); Honan Island, C. O. Levine, no. 1209, August 25, 1917 (G); Hoihow, F. A. McClure, no. 7618, Oct. 12, 1921 (vine 1-7 meters; flowers white, blue, lavender, very fragrant; fruit black) (AA); Honan Island, C. O. Levine, no. 208, Dec. 30 (1916) (AA); precise data lacking, Mrs. S. W. Williams (G, NY). British India: Mt. Sylhet, Assam, N. Wallich, no. 2853 (AA, photo. of type from Br).

Most of the previously determined material of *J. amplexicaule* Buch.-Ham. has been labeled either *J. undulatum* Willd. or *J. undulatum* Ker-Gawl. Willdenow described the first and original *J. undulatum* in Spec. Pl. which material later was found to be conspecific with *J. sambac* Ait. Ker-Gawler with material distinctly different illustrated and discussed the present species under the name *J. undulatum* thinking it to be the same. Later after the original *J. undulatum* of Willd. had been transferred to *J. sambac* botanists encountering the material illustrated by Ker-Gawler continued calling it *J. undulatum*, accrediting, however, the authorship to Ker-Gawler. Under the present International Rules this latter name is invalidated being a later homonym and it is necessary to accept the name *J. amplexicaule* proposed by Buchanan-Hamilton in 1829, which up to this time has been considered a synonym of Ker-Gawler's species.

26a. *Jasminum amplexicaule* Buch.-Ham. var. *elegans* (Hemsl.). comb. nov.

Jasminum undulatum Ker var. *elegans* Hemsley in Jour. Linn. Soc. xxvi. 81 (1889).

K w a n t u n g : Pakhoi, *Playfair* (ex Hemsley, l. c.).

Hemsley in the original description of this variety cited material from both Kwantung and Formosa. In the herbarium of the Arnold Arboretum, no material from Kwantung can be found. However, Wilson's nos. 10296 and 11132 and Henry's no. 639 from Formosa all representing this variety are available at the Arnold Arboretum.

LISTS OF COLLECTORS NUMBERS

- | | |
|--|---|
| AITCHISON, J. E. T. | CLEMENS, J. & M. S. |
| 289. <i>J. humile</i> | 3448. <i>J. lanceolarium</i> |
| D'ARGY, CH. | DUCLOUX, F. |
| —, <i>J. floridum</i> | 6. <i>J. Beesianum</i> |
| BOCK, C. & A. v. ROSTHORN | 58. <i>J. polyanthum</i> |
| 163. <i>J. floridum</i> | 112. <i>J. dumicolum</i> |
| 1151. <i>J. floridum</i> | 165. <i>J. Mesnyi</i> |
| CAVALERIE, J. | 483. <i>J. Beesianum</i> |
| 3038. <i>J. sinense</i> | 800. <i>J. polyanthum</i> |
| 3912. <i>J. polyanthum</i> | 7175. <i>J. Mesnyi</i> |
| —, <i>J. Prainii</i> | ESQUIROL, J. |
| CHIAO, C. Y. | 729. <i>J. multiflorum</i> |
| 2583. <i>J. nudiflorum</i> | 887. <i>J. lanceolarium</i> var. <i>puberulum</i> |
| CHING, R. C. | —, <i>J. polyanthum</i> |
| 1890. <i>J. lanceolarium</i> var. <i>puberulum</i> | FABER, ERNST |
| 3313. <i>J. lanceolarium</i> | 47. <i>J. urophyllum</i> |
| 5175. <i>J. anastomosans</i> | FANG, W. P. |
| 5394. <i>J. sambac</i> | 788. <i>J. floridum</i> |
| 5970. <i>J. lanceolarium</i> var. <i>puberulum</i> | 2196. <i>J. urophyllum</i> |
| 6282. <i>J. lanceolarium</i> | 4239. <i>J. floridum</i> |
| 6667. <i>J. multiflorum</i> | 5666. <i>J. lanceolarium</i> |
| 6954. <i>J. lanceolarium</i> | FORD, C. |
| 7023. <i>J. sinense</i> | 113. <i>J. microcalyx</i> |
| 7521. <i>J. pentaneurum</i> | —, <i>J. amplexicaule</i> |
| CHUN, W. Y. | —, <i>J. lanceolarium</i> |
| 3088. <i>J. lanceolarium</i> | —, <i>J. lanceolarium</i> |
| 3468. <i>J. floridum</i> | —, <i>J. pentaneurum</i> |
| 3572. <i>J. floridum</i> | —, <i>J. sinense</i> |
| 3845. <i>J. lanceolarium</i> var. <i>puberulum</i> | FORREST, G. |
| 5670. <i>J. lanceolarium</i> var. <i>puberulum</i> | 2021. <i>J. Beesianum</i> |
| 6344. <i>J. pentaneurum</i> | 4658. <i>J. polyanthum</i> |
| 6911. <i>J. lanceolarium</i> | 4659. <i>J. humile</i> |
| 7470. <i>J. lanceolarium</i> | 4683. <i>J. officinale</i> f. <i>grandiflorum</i> |
| 30472. <i>J. pentaneurum</i> | 5529. <i>J. heterophyllum</i> var. <i>subhumile</i> |
| CHUNG, H. H. | 7861. <i>J. sinense</i> |
| 959. <i>J. sinense</i> | 7926. <i>J. dumicolum</i> |
| 3585. <i>J. lanceolarium</i> var. <i>puberulum</i> | 8072. <i>J. lanceolarium</i> |
| 3836. <i>J. sambac</i> | 8094. <i>J. dumicolum</i> |
| | 8136. <i>J. urophyllum</i> var. <i>Wilsonii</i> |
| | 9346. <i>J. dumicolum</i> |

9531. *J. dumicolum*
 9744. *J. Mesnyi*
 9757. *J. dumicolum*
 9761. *J. polyanthum*
 9873. *J. heterophyllum* var. *subhumile*
 9955. *J. Mesnyi*
 9990. *J. heterophyllum* var. *glabricorymbosum*
 10066. *J. Beesianum*
 10107. *J. officinale*
 11037. *J. heterophyllum* var. *glabricorymbosum*
 11177. *J. heterophyllum* var. *glabricorymbosum*
 11472. *J. heterophyllum* var. *glabricorymbosum*
 11667. *J. Seguinii*
 11827. *J. lanceolarium*
 13832. *J. humile*
 13834. *J. nudiflorum* var. *pulvinatum*
 14478. *J. nudiflorum* var. *pulvinatum*
 15605. *J. Seguinii*
 15720. *J. dispersum*
 16193. *J. nudiflorum* var. *pulvinatum*
 18330. *J. Seguinii*
 18927. *J. humile*
 19251. *J. humile*
 19296. *J. officinale*
 19666. *J. nudiflorum* var. *pulvinatum*
 20004. *J. nudiflorum* var. *pulvinatum*
 20417. *J. officinale*
 23166. *J. Seguinii*
 GAMME, G. A.
 —. *J. officinale* f. *grandiflorum*
 GING, T. S.
 5196. *J. sambac*
 GIRALDI, J.
 1519. *J. Giraldii*
 —. *J. Giraldii*
 GROFF, G. W.
 11501. *J. multiflorum*
 HANDEL-MAZZETTI, H.
 20. *J. Beesianum*
 5827. *J. coffeinum*
 8613. *J. Mesnyi*
 10649. *J. lanceolarium* var. *puberulum*
 11010. *J. sinense*
 HELFER, J. W.
 3718. *J. officinale* f. *grandiflorum*
 HENRY, A.
 940. *J. lanceolarium*
 2700. *J. floridum*
 2729. *J. lanceolarium* var. *puberulum*
 3000. *J. lanceolarium* var. *puberulum*
 3669. *J. lanceolarium* var. *puberulum*
 4469. *J. sinense*
 4562. *J. lanceolarium* var. *puberulum*
 6288. *J. floridum*
 8456. *J. anastomosans*
 9107. *J. heterophyllum* var. *glabricorymbosum*
 9107A. *J. heterophyllum* var. *glabricorymbosum*
 9107B. *J. heterophyllum* var. *glabricorymbosum*
 9319. *J. Mesnyi*
 9319A. *J. Mesnyi*
 9433. *J. nintoooides*
 9433A. *J. nintoooides*
 9433B. *J. nintoooides*
 9581. *J. Seguinii*
 9581B. *J. Seguinii*
 9581C. *J. Seguinii*
 9657. *J. sinense*
 9657A. *J. sinense*
 9657B. *J. sinense*
 10314. *J. polyanthum*
 10314A. *J. polyanthum*
 10314B. *J. polyanthum*
 10634A. *J. dumicolum*
 10887. *J. coarctatum*
 11656. *J. polyanthum*
 11708. *J. dumicolum*
 11653. *J. coarctatum*
 11653A. *J. coarctatum*
 11713. *J. lanceolarium*
 11969. *J. anastomosans*
 12661. *J. Seguinii*
 12661A. *J. Seguinii*
 13354. *J. sinense*
 13397. *J. officinale* f. *grandiflorum*
 —. *J. floridum*
 HENRY, B. C.
 22171. *J. microcalyx*
 HERS, J.
 2440. *J. Giraldii*
 HO, H. T.
 60041. *J. pentaneurum*
 HOOKER, J. D.
 —. *J. humile*
 —. *J. dispersum*
 HOOKER, W. J.
 Cat. no. 12246. *J. officinale* f. *grandiflorum*

- HU, H. H.
 426. *J. lanceolarium* var. *puberulum*
 1065. *J. lanceolarium*
- HUI, W. T.
 202. *J. lanceolarium* var. *puberulum*
- INAYAT,
 ——. *J. officinale* f. *grandiflorum*
- JENKINS, COLONEL
 ——. *J. coarctatum*
- KANJILAL, U.
 4656. *J. dispersum*
- KATSUMATRA,
 5406. *J. anastomosans*
- KENG, Y. L.
 218. *J. lanceolarium* var. *puberulum*
- KESHAVANAM,
 657. *J. officinale* f. *grandiflorum*
- KING, DR. G.
 220. *J. dispersum*
 ——. *J. dispersum*
- LABORDE, J.
 ——. *J. sinense*
- LEVINE, C. O.
 208. *J. amplexicaule*
 910. *J. sambac*
 1209. *J. amplexicaule*
 2016. *J. pentaneurum*
 3107. *J. lanceolarium*
 3180. *J. pentaneurum*
 3320. *J. sinense*
- LEVINE, C. O. & G. W. GROFF
 42. *J. pentaneurum*
 163. *J. lanceolarium*
- LIMPRICHT, W.
 2006. *J. Beesianum*
 2689. *J. Giralddii*
- MAIRE, E. E.
 108. *J. Beesianum*
 199. *J. Mesnyi*
 245. *J. humile*
 253. *J. polyanthum*
 451. *J. humile*
 3310. *J. Beesianum*
 3352. *J. officinale*
 7188. *J. officinale* f. *grandiflorum*
 7417. *J. Beesianum*
 ——. *J. Beesianum*
 ——. *J. humile*
 ——. *J. humile*
- MCCLURE, F. A.
 2353. *J. amplexicaule*
 7595. *J. microcalyx*
 7618. *J. amplexicaule*
 9193. *J. anastomosans*
- MELL, R.
 62. *J. lanceolarium*
 215. *J. pentaneurum*
 922. *J. pentaneurum*
- MERRILL, E. D.
 10693. *J. lanceolarium*
- MESNY, W.
 21211. *J. Mesnyi*
- MEYER, F. N.
 1817. *J. floridum*
- PARKER, R. N.
 2979. *J. officinale* f. *grandiflorum*
 ——. *J. dispersum*
 ——. *J. humile*
 ——. *J. officinale*
- PRAIN, DR. D.
 892. *J. lanceolarium*
- PURDOM, WM.
 368. *J. Giralddii*
 907. *J. Giralddii*
 908. *J. Giralddii*
- RAM, BIS
 124. *J. dispersum*
 147. *J. humile*
 326. *J. dispersum*
 360. *J. humile*
 452. *J. officinale*
 460. *J. dispersum*
 462. *J. humile*
- RAWAT, C. S.
 76. *J. dispersum*
- ROCK, J. F.
 2416. *J. coarctatum*
 2440. *J. Seguinii*
 2507. *J. anastomosans*
 2611. *J. anastomosans*
 2763. *J. coarctatum*
 2781. *J. coarctatum*
 2829. *J. Mesnyi*
 2934. *J. lanceolarium*
 3016. *J. dispersum*
 3016. *J. heterophyllum* var. *glaberrimum*
 3069. *J. lanceolarium*
 3190. *J. officinale*
 3216. *J. Beesianum*
 3244. *J. officinale*
 3293. *J. humile*
 3312. *J. officinale*
 3879. *J. heterophyllum* var. *glaberrimum*
 3955. *J. heterophyllum* var. *glaberrimum*
 4509. *J. stephanense*
 6214. *J. Seguinii*
 7833. *J. lanceolarium*
 7894. *J. dumicolum*

8033. *J. heterophyllum* var. *glabricorymbosum*
 8292. *J. heterophyllum* var. *glabricorymbosum*
 8539. *J. heterophyllum* var. *glabricorymbosum*
 8896. *J. nudiflorum* var. *pulvinatum*
 10602. *J. heterophyllum* var. *glabricorymbosum*
 14653. *J. humile*
 14797. *J. humile*
 15035. *J. humile*
 ROYLE, DR. J. F.
 ——. *J. officinale*
 RUSE, L. F.
 135. *J. lanceolarium*
 SCHNEIDER, C. K.
 32. *J. Mesnyi*
 486. *J. Mesnyi*
 702. *J. officinale*
 905. *J. Beesianum*
 973. *J. Beesianum*
 1137. *J. Seguinii*
 1302. *J. humile*
 1474. *J. officinale*
 2082. *J. Beesianum*
 2150. *J. Seguinii*
 3199. *J. Beesianum*
 3222. *J. humile*
 3264. *J. humile*
 4091. *J. humile*
 SCHOCH, O.
 18. *J. polyanthum*
 36. *J. humile*
 206. *J. officinale*
 207. *J. Beesianum*
 SEGUIN, J.
 2354. *J. Seguinii*
 SKATCHKOV, C. A.
 ——. *J. floridum*
 SMITH, HARRY
 1583. *J. Mesnyi*
 1622. *J. polyanthum*
 1886. *J. Beesianum*
 1890. *J. humile*
 2463. *J. humile*
 5508. *J. nudiflorum*
 STEWART, R. R.
 2467. *J. humile*
 6228. *J. officinale* f. *grandiflorum*
 STRACHEY, R. & J. E. WINTERBOTOM
 1. *J. humile*
 2. *J. humile*
 5. *J. officinale* f. *grandiflorum*
 6. *J. dispersum*
 TAK, TSANG WAI
 16718. *J. lanceolarium*
 TÊN, SIMEON
 99. *J. heterophyllum* var. *glabricorymbosum*
 131. *J. Seguinii*
 375. *J. humile*
 499. *J. Beesianum*
 515. *J. humile*
 THOMSON, T.
 ——. *J. dispersum*
 ——. *J. humile*
 ——. *J. officinale*
 To, AH
 3177. *J. pentaneurum*
 TSIANG, Y.
 417. *J. amplexicaule*
 1143. *J. pentaneurum*
 1490. *J. pentaneurum*
 1574. *J. multiflorum*
 1615. *J. amplexicaule*
 2221. *J. anastomosans*
 2244. *J. anastomosans*
 2244A. *J. pentaneurum*
 2292. *J. amplexicaule*
 2437. *J. amplexicaule*
 2544. *J. anastomosans*
 2573. *J. amplexicaule*
 2970. *J. lanceolarium*
 3005. *J. lanceolarium*
 Tso, C. L.
 21001. *J. lanceolarium* var. *puberulum*
 TSU, L. F.
 629. *J. floridum*
 WALLICH, N.
 2853. *J. amplexicaule*
 WANG, Y. K.
 321. *J. pentaneurum*
 1832. *J. pentaneurum*
 3206. *J. lanceolarium*
 3219. *J. lanceolarium*
 WIGHT, ROBERT
 1752. *J. officinale* f. *grandiflorum*
 WILSON E. H. (ARNOLD ARBORETUM EXPED.)
 598. *J. Giraldii*
 781. *J. lanceolarium*
 781A. *J. lanceolarium* var. *puberulum*
 789 in part. *J. floridum*
 1122. *J. urophyllum*
 2807. *J. officinale*
 2808. *J. sinense*
 2809. *J. humile*
 ——. *J. humile*

WILSON, E. H. (VEITCH EXPED.)

83. *J. floridum*1018. *J. lanceolarium* var. *puberulum*1499. *J. urophyllum* var. *Wilsonii*1576. *J. sinense*4074. *J. Beesianum*4074A. *J. officinale*4075. *J. urophyllum* var. *Wilsonii*HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.4077. *J. humile*4078. *J. humile*5042. *J. lanceolarium*

WILLIAMS, MRS. S. W.

— . *J. amplexicaule*

WRIGHT, C.

— . *J. lanceolarium*

ZIMMERMANN, R.

296. *J. nudiflorum*

THE CYTOLOGICAL MECHANISM OF CROSSING OVER

KARL SAX

With plate 44, one text figure and 11 diagrams

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INTRODUCTION

Two theories concerning the mechanism of crossing over have recently been advanced. The first theory is essentially the "partial chiasmotypy" hypothesis of Janssen's (1924), which is based on the assumption that chiasmata are caused by crossing over between two of the four chromatids. This theory has been sponsored by Belling (1929, 1931, a. b.), Darlington (1930, 1931) and Maeda (1930). The other theory of crossing over is based on the assumption that chiasmata do not represent crossovers, but are caused by an alternate opening out of sister and non-sister chromatids at diplotene (Weinrich 1916; Robertson 1916; Wilson 1925; Seiler 1926; McClung 1927; Belar 1928). A crossover occurs only when two chromatids break at a chiasma (Sax 1930).

An analysis of chromosome behavior at meiosis and an analysis of crossover types in the attached X chromosomes in *Drosophila melanogaster* should afford some critical evidence for a comparison of the two theories of the cytological mechanism of crossing over. This work is based on a cytological study of the chromosomes of *Callisia repens*, a survey of chiasma frequency in other plant genera, and an analysis of some of the genetic evidence obtained from *Drosophila*.

CHROMOSOME BEHAVIOR IN *CALLISIA REPENS*

In *Callisia repens* it is possible to follow the behavior of the chromosomes at all stages from pachytene to metaphase. This

material was collected and preparations made at the Harvard Botanic Garden, Soledad, Cuba. The writer is indebted to Professor Oakes Ames, Supervisor of the Arnold Arboretum and the Harvard Botanic Garden, for making possible the trip to Cuba.

Callisia repens has six pairs of large chromosomes. In two pairs of chromosomes the spindle fiber attachment points are more or less median while the other four pairs have nearly terminal fiber attachments. The twelve somatic chromosomes are shown in text-figure 1. The chromosome in the middle of the metaphase plate has one



FIG. 1. CHROMOSOMES OF *CALLISIA REPENS*

arm oriented at right angles to the plane of the other chromosomes. The sister chromatids in many of the chromosomes are clearly separated and show little twisting about each other. The limited number of twists or half twists in the somatic chromosomes is of special interest in connection with the theories of crossing over.

The study of meiotic chromosomes is based on smear preparations of pollen mother cells fixed in Navaschin's solution and stained with crystal violet iodine. The figures in the plate were drawn at a magnification of 3100 diameters and reduced about one-fourth in reproduction.

During the early pachytene stage the spireme is so compact that individual chromosomes cannot be identified. A small nucleolus is always present and is almost invariably at the periphery of the spireme and in contact with a free end of a chromosome thread. As the spireme opens up it is evident that it consists of six long inter-looped chromosomes (Plate 44, fig. 1). The end of one of the shorter chromosomes is invariably in contact with the nucleolus. At a somewhat later stage the six bivalent chromosomes, still paired throughout their length, can be easily recognized. This stage is shown in figure 2. The two long bivalents are numbered 2 and 5. One of the short chromosomes, number 3, appears to have started

opening out into the typical nodes and internodes of the diplotene stage. The nodes and internodes at this stage appear to be much more numerous than at late diplotene.

The chromosomes shown in figure 3 have in most cases opened out into the diplotene loops, although parts of several chromosomes appear to have remained closely paired as they were at the typical pachytene stage. The nucleolus shows considerable disintegration at this stage and usually the side away from the chromosome attachment disappears first. The nucleolus is attached to one of the shorter chromosomes in all cases and it seems very probable that the same chromosome is always associated with the nucleolus.

When all of the chromosomes have reached the diplotene stage the number of nodes per chromosome ranged from two to more than five. It is not possible to recognize the individual chromatids in this material so that it is impossible to be sure that all of the nodes are chiasmata, but judging from the association of chromatids in *Orthoptera* chromosomes and at later stages in plant species it seems probable that most of them are chiasmata. The total number of nodes or chiasmata at diplotene is about twenty-five or an average of somewhat more than four per bivalent (Fig. 4.)

At early diakinesis the chromosomes become much thicker and shorter. An intermediate stage is shown in figure 5. The number of nodes or chiasmata is reduced to a total of about ten. The two long chromosomes seem to show some evidence of fiber constriction points but for the most part these constrictions do not show. Later stages of diakinesis are shown in figures 6 and 7. The total number of nodes is now at a minimum and no further reduction takes place before the chromosomes are separated at the first meiotic division.

The individual chromatids are not distinguishable even at the first metaphase but the configuration of the bivalents shows the number of attachment points. The chromonemata are distinctly coiled in some cases, but are not sufficiently clear for a critical study of the association of chromatids (Fig. 8). At telophase two of the daughter chromosomes have four arms since the fiber attachment is more or less median, while the other four daughter chromosomes consist of the two sister chromatids attached at one end by the fiber constriction (Fig. 9). The nucleolus disappears at metaphase.

The constant association of the nucleolus with one of the shorter chromosomes enables this particular chromosome to be recognized at all stages up to metaphase. This chromosome at late pachytene is shown at the left in figure 10 to show the relative amount of contraction which occurs between pachytene and late diakinesis. The

decrease in length is somewhat more than one-half. Five of the marked chromosomes are shown at the diplotene stage (Fig. 10) for comparison with the same chromosomes at diakinesis (Fig. 11—the five chromosomes to the right). An intermediate stage is also included at the left. It is apparent that there is considerable reduction in the number of nodes, most of which are presumably chiasmata, between diplotene and diakinesis. In the five diplotene chromosomes the average number of nodes is about three per chromosome, while at diakinesis it is only a little more than one per bivalent. An examination of 26 of these marked chromosomes at diplotene showed an average of 2.1 nodes per bivalent while 28 bivalents at diakinesis had an average of 1.1 nodes or chiasmata. For these short chromosomes the reduction of nodes is about 1 per bivalent, or one-half of the nodes formed at diplotene. The long chromosomes may have as many as four or five nodes at diplotene but seldom more than two at diakinesis.

While this evidence is not conclusive it does indicate that there is considerable reduction in the number of chiasmata between early diplotene and the first meiotic metaphase stage.

THE BEHAVIOR OF THE NUCLEOLUS

At the earliest prophase stages of meiosis in *Callisia* only one nucleolus is observed. The nucleolus is almost invariably at the periphery of the spireme and attached to the end of a spireme thread. As soon as the spireme is opened up enough to follow the threads it is found that no continuous spireme exists. There are six distinct chromosomes at this stage and the nucleolus is attached to one of these chromosomes, and later stages show that the same chromosome is always involved. As the chromosomes contract the nucleolus disintegrates and it finally disappears at metaphase.

It is apparent that the nucleolar contents cannot pass into the entire spireme thread. It is doubtful if the spireme thread is ever continuous in either the somatic or meiotic prophases of *Callisia*. The fact that the nucleolus disappears or decreases in size and staining capacity as the chromosomes develop has led to the belief that the nucleolar material is absorbed by the chromosomes. A review of the work on nucleolar activity has recently been presented by Zirkle (1931) and by Fikry (1930).

Fikry has presented what appears to be a logical explanation of the relation between nucleoli and chromosomes, and this interpretation seems to have considerable cytological support. The gene string builds up a surrounding sheath of chromatin as the chromosomes develop from early prophase. Each gene builds up its own

specific enzyme complex. At telophase this chromatic product is released from the gene strings, or chromatids, to form the nucleolus. In the next division the nucleolar substance passes out into the cytoplasm carrying with it the specific gene enzymes or enzyme products.

Certainly this theory offers an attractive hypothesis to account for the transmission of gene activity to the cytoplasm. The genes develop a chromatin sheath which is later differentiated into the more chromatic chromonemata and the more or less diffuse chromatin or oxychromatin. As the chromosomes pass to the poles at telophase the chromosome sheaths or pellicles fuse to form the nuclear membrane and the more fluid chromatin matrix is released to form nucleoli (Bridges in Alexander 1928). In cases where the chromosomes are not closely associated at telophase, as in the gymnosperms, many nucleoli are formed, but in most angiosperms the chromosomes are compact at telophase and the released oxychromatin fuses to form one or two nucleoli. The nucleoli become still further transformed so that they no longer take the typical chromatin stains (Zirkle 1931). As the chromosomes develop for the next division the nucleolus usually disintegrates and when the nuclear wall breaks down the products of the nucleolus become incorporated in the cytoplasm. Occasionally the nucleolus persists until metaphase where it may pass to one pole, or divide and pass to both poles, but in either case it usually passes into the cytoplasm and is absorbed. (Yamaha and Sinoto 1925.)

THE MECHANISM OF CROSSING OVER

A modification of Janssen's (1924) "partial chiasmotypy" theory of crossing over has recently been sponsored by Darlington (1930), Maeda (1930) and Belling (1931, a. b.). This theory postulates that a chiasma is caused by crossing over between two of the four chro-

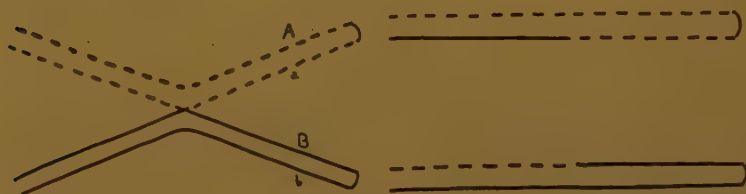


DIAGRAM 1

matids at pachytene. At diplotene the chiasmata represent cross-overs and only sister chromatids are paired as shown in diagram 1. When the homologues are separated at metaphase the crossover at

the chiasma will result in two non-crossover chromatids and two crossover chromatids. Every chiasma represents a crossover, but according to Maeda and Belling every point of contact or node at diplotene is not necessarily a chiasma, but may be an overlap or temporary fusion of the paired chromatids. The assumptions upon which this theory is based have been criticized by McClung (1927). The more recent arguments of Belling and Darlington will be considered later in this paper.

In 1930 the writer presented an hypothesis to account for the mechanism of crossing over which seems to have considerable cytological support and is in accord with the genetic requirements. This theory is based on the usual assumption that chiasmata are formed by the alternate opening out of sister and non-sister chromatids at diplotene. A crossover is caused by a break in the two crossed chromatids at a chiasma between diplotene and late diakinesis. (Diagram 2.)



DIAGRAM 2

It is assumed that sister chromatids are always associated at the spindle fiber attachments during the first meiotic division, which is in accord with both the cytological and genetic evidence. The second meiotic division separates the sister chromatids and is an equational division for regions of the chromosome between the spindle fiber and the first crossover.

The paired chromatids are assumed to be associated, gene by gene, throughout their length, so that a crossover usually occurs between the same two consecutive genes in each chromatid as shown in diagram 3. The spindle fiber is to the right and is terminal.



DIAGRAM 3

In rare cases unequal crossing over occurs (Sturtevant 1925, 1928, Morgan 1931) which can be accounted for if the genes in the region

of the chiasma are not closely paired. In such a case crossing over need not occur between the same two consecutive genes in each chromatid, but may result in gene duplication and deficiency as shown in diagram 4.



DIAGRAM 4

Gene duplication and deficiency occur in case of the bar gene in the X chromosome of *Drosophila* only when there is crossing over between forked and fused, so Sturtevant concluded that crossing over does not occur between sister chromatids in this region of the X chromosome. The order of the two duplicated genes bar and infrabar may be BB' or B'B. In diagram 4 the order of these genes is BB' but if the chromatids cross and break above these two genes the order will be B'B. All of these genetic observations can readily be explained on the writer's hypothesis.

Crossing over between sister chromatids, according to this theory, cannot occur before the first regular genetically detectable crossover, and at other points can occur only when a half twist occurs in one pair of sister chromatids accompanied by an opening out of non-sister pairs of chromatids on both sides of the half twist. (Diagram 5.)



DIAGRAM 5

The first crossover from the spindle fiber end of the chromosome would invariably occur between non-sister chromatids, but in some cases subsequent crossovers might occur between sister threads. Thus there would be little chance for a sister thread crossover to occur at the bar locus in the X chromosome of *Drosophila* because bar is only about 12 units from the fiber attachment point. The hypothesis is again in accord with the genetic observation that crossing over does not occur between sister chromatids at the bar locus (Sturtevant 1928).

Factors which suppress crossing over in *Drosophila* (Gowen 1922, 1928) also inhibit chromosome pairing. Crossover reducers are known to be caused by inverted segments (Sturtevant 1926) trans-

locations (Dobzhansky 1931) and may be caused by deficiencies. Any factor which inhibits chromosome pairing would of course decrease or eliminate crossing over between homologous chromosomes on either theory of crossing over.

JANSSEN'S "PARTIAL CHIASMATYPY" HYPOTHESIS

According to Darlington (1930) "partial chiasmotypy," which demands crossing over between two of the four chromatids at every chiasma, is the only possible working hypothesis for the correlation of the cytological and genetical observations." Darlington's argument is based on the types of chromosome association in triploids and tetraploids. The drawings and diagrams in his 1930 paper "are the result of a special search for the missing configuration in this critical material." In *Tulipa* and *Hyacinthus* triploid chromosomes were occasionally found to be associated as shown in diagram 6. A third chromosome intercalated between two chiasmata of a bivalent by a single chiasma is assumed to be critical evidence that this chiasma is caused by a previous crossover between two chromatids. If a third chromosome in triploids is invariably intercalated between two chiasmata in the other two chromosomes by a single chiasma there might be some justification for Darlington's conclusion, but since the frequency of such types is not known, the evidence presented is not critical.

These types of trivalents can also be explained on the assumption that chiasmata are caused by alternate opening out of sister and non-sister chromatids and that one chiasma disappears before diakinesis due to breaks in the chromatids as shown in diagram 7.



DIAGRAMS 6 AND 7

According to this theory of chiasma formation chromosome C must form two chiasmata with chromosome B. But if one of these chiasmata frequently breaks, as would be expected according to the writer's theory of crossing over, then at diakinesis chromosome C will often be associated with B only by a single chiasma. Darlington's tetraploid configurations and *Oenothera* figure 8 chromosomes (Darlington 1931 B) can be interpreted in the same way, and cannot

be considered as critical evidence in favor of Janssen's partial chiasmatty theory of crossing over.

If all three homologous chromosomes in triploids can pair simultaneously at the same locus, as Belling has described in *Hyacinthus*, then Darlington's "critical" figures could be obtained without any crossing over.

In a later paper Darlington (1931a) attempts to correlate the frequency of chiasma formation with the percentage of crossing over in *Primula sinensis*. The SBGL chromosome, which is assumed to be one of the longest chromosomes of *Primula sinensis*, was estimated from crossover data, to be 111.6 genetic units long, but this may be incorrect since Haldane's (1919) correction of map distance is not valid (Morgan, Bridges and Sturtevant 1925).

According to Darlington's theory of crossing over each chiasma will result in 50 per cent crossing over and the length of a chromosome in genetic units can be calculated as $50 \times$ the number of chiasmata. Darlington finds an average of 3.5 chiasmata per bivalent which he considers may be an under-estimate for the longest chromosomes. Due to an error, Darlington calculated the crossover length, based on number of chiasmata, as 58.3 to 116.7 units, which he says is "in strict agreement with expectation." But the correct length based on chiasma frequency, should be 3.5×50 or 175 units as an average, or to range from 116.7 to 233.4 units, as Darlington later discovered. Obviously the length of the longest chromosome as measured by crossing over is only about half as long as the length expected, if each chiasma represents a crossover.

On the writer's theory of crossing over, chromosome SBGL should be somewhat more than 100 units long which is "in strict agreement with expectation"! It is probable however, that neither the genetic nor the cytological data are adequate for any serious calculation of the crossover length of any of the chromosomes in *Primula*.

In order to explain the absence of crossing over in the *Drosophila* male, Darlington (1931 a) assumes that there are always two chiasmata in each bivalent, that the two chiasmata are very close together, that no mutations occur in the region between chiasmata, that the spindle fiber attachment point is between the chiasmata, and that the double crossover invariably involves the same two chromatids. All of these assumptions are highly improbable, and the assumption that the two crossovers are always reciprocal is not in accord with the genetic evidence.

On the alternative theory of crossing over, it is assumed that in the *Drosophila* male, chiasmata are formed as they are in the female, although perhaps less frequently, and that chromosome develop-

ment from diplotene to metaphase is sufficiently gradual so that the chromatids can adapt themselves to the changes without breaking. A gradual development would permit the chromatids to contract as the chromosomes contract so that no coiling of the chromonemata would occur. The chiasmata would be free to terminalize without breaks in the chromatids, as seems to be the case in the Orthopteran chromosomes. Since terminalization is easily effected the meiotic metaphase in the male should be of short duration as compared with the same stage in the female, as seems to be the case (Huettner 1930). The reverse would be the case according to Darlington's theory. Crossing over in the female is most frequent towards the ends of the second and third chromosomes of *Drosophila melanogaster* so that only two subterminal chiasmata would usually need to be pulled apart, but in the male the two reciprocal chiasmata near the spindle fiber would have to be terminalized for practically the entire length of the chromosomes.

Darlington does not attempt to explain why breaks occur in the chromatids at pachytene, why the breaks in the crossover chromatids almost invariably occur at the same level, why chromatids should recombine in new association after they break, why only two chromatids cross over at any one locus, or why one crossover interferes with the occurrence of a second one in the same region.

According to Darlington, at least one chiasma is essential for pairing of homologous chromosomes and every chiasma represents a crossover. Therefore, crossing over must be universal in all normal species and no normal chromosome can be less than 50 genetic units long. No explanation has been presented to account for the behavior of the fourth chromosome of *Drosophila melanogaster*. This chromosome is about as regular in conjugation and disjunction as the X chromosome, but no crossing over occurs in the fourth chromosome. There are also other obvious objections to Darlington's theory of chromosome pairing (O'Mara, in press).

BELLING'S THEORY OF CROSSING OVER

Belling (1931 a) has recently presented an hypothesis to account for the mechanism of crossing over. The homologous chromosomes pair as single chromatids. Half twists occur in the paired homologues at early pachytene before the secondary split has begun. When the secondary split occurs the new chromomeres must form new connecting fibers and at each twist they take the shortest route in connecting adjacent chromomeres. Thus crossing over would occur only between the two new chromatids formed at late pachytene. This interpretation is obviously invalid because in *Drosophila*

crossing over is found in more than 50 per cent of the emerging X chromosomes, and nearly 75 per cent of the third chromosomes have one or more crossovers (Redfield 1930).

More recently Belling's (1931 b) modified his hypothesis. This new theory seems to be plausible since it accounts for crossing over between any two chromatids, and provides a mechanism to explain translocations and inversions in somatic chromosomes. If Janssen's partial chiasmotypy theory of crossing over is correct Belling's hypothesis of the mechanism involved would seem to be the only logical explanation. Unfortunately there are a number of serious objections to this theory.

According to Belling a half twist between single chromatids occurs at pachytene. When the new chromomeres are produced at the secondary split the connecting fiber between genes may remain with the old gene (genes and chromomeres are assumed to be synonymous) according to the laws of chance. The new connecting fibers then unite the free genes by the shortest path (Diagram 8).



DIAGRAM 8

As shown in the diagram 8, the new connecting fibers may result in a crossover between a' and b' or between a' and b . If the connecting fibers remain with the old genes or pass to the new ones at random there will be random crossing over between any two of the four chromatids.

Random assortment of connecting fibers would also mean that in both somatic and meiotic chromosomes crossing over between sister threads would be very frequent. In a chromosome containing a hundred genes 50 sister crossovers would be expected. In the somatic chromosomes this sister crossing over would result in much twisting of the two chromatids at late prophase and at metaphase, if the new connecting fibers which unite old and new genes pass at random on either side of the old connecting fiber. But there are only a limited number of twists or half twists in the somatic chromosomes (text figure 1) and between paired chromatids at meiosis (Seiler, 1926).

Belling's theory is also based on the assumption that the homologous chromosomes first pair as single chromatids at meiosis. The work of Kaufmann (1926) and Sharp (1929) seems to show that the

somatic chromosomes in certain plant species are already split into two chromatids at the preceding anaphase. According to Kaufmann (1931) the chromosomes at the telophase of the last premeiotic division show the parallel chromonemata. In *Paratettix*, the chromosomes are split longitudinally when they enter the spermatid (Robertson, 1931 a), and Robertson (1931 b), also shows that the homologous chromosomes in the *Tettigidae* are already divided into sister chromatids when they begin pairing at meiosis. Similar observations have previously been made by Robertson (1916) and McClung (1928). These observations cannot be reconciled either with Belling's theory of crossing over, or with Darlington's (1931) theory of meiosis.

One other point in comparing the two theories has been presented by Belling (1931 b) in connection with the behavior of unequal homologues. One pair of unequal homologues were found in *Aloe purpurascens*. If chiasmata are formed by the alternate opening out of sister and non-sister pairs of chromatids, in some cases a short arm should be associated with a long one at diplotene or diakinesis, but no such association was found. On Belling's hypothesis no pairing of long and short arms would be expected since only sister chromatids are paired at diplotene. If the chiasma is to the distal side of the fiber constriction, as shown in diagram 9b, then a short and a long arm should be associated on the writer's hypothesis, unless a crossover had occurred. On Belling's hypothesis such a chiasma (9a) should invariably result in a distribution of a long and a short chromosome to each pole at the first meiotic division, but Belling observes that "in some cases they are observed to separate into short plus long and short plus long chromatids."



DIAGRAM 9

If, in most cases, the segregation at anaphase is into two short and two long homologues, as Belling's statement would imply, then the chiasma must be to the right of the fiber attachment point (9c) or the homologues are terminally associated without chiasma formation. On the writer's hypothesis a chiasma to the right of the fiber constriction (9b) or a terminal association of chromosomes, would result in the observed association of chromatids—short with short and long with long at diplotene. It is evident that Belling's obser-

vations are inadequate for any critical test of the method of chiasma formation.

REDUCTION IN NUMBER OF CHIASMATA

The writer's theory of crossing over postulates breaks in the chiasmata so that a decrease in the number of chiasmata would be expected between early diplotene and metaphase if crossing over occurs.

At early diplotene, as the homologous chromonemata open out, the nodes and internodes are often very numerous. This condition is indicated in chromosome number 3 in figure 2, and is clearly shown in *Lathyrus* (Maeda, 1930, Fig. 17 B) and in *Zea* (Cooper and Brink 1931, Fig. 1). These nodes may be chiasmata, most of which subsequently meet as the homologous chromonemata open out more completely at the internodes. There is also a possibility that some of these nodes which disappear are due to breaks in chiasmata at this stage of meiosis. Since the individual chromatids cannot be identified many of these early nodes may be only temporary adhesions as Belling has suggested.

In *Tulipa* Newton (1926) pictures about 30 chiasmata in 11 diplotene chromosomes (Fig. 25). At early diakinesis the number of chiasmata are especially clear, and show a total of about 27 chiasmata for the 12 chromosomes (Fig. 31) while at late diakinesis Newton found only 15 chiasmata (Fig. 30). Thus the average number of nodes or chiasmata per bivalent chromosome is reduced from almost 3 at diplotene to only 1.25 at late diakinesis.

In *Lilium longiflorum*, Belling (1928) found a decrease in number of nodes between diplotene and late diakinesis of 43 per cent and suggests that more nodes would have been found if counts could have been made at an earlier stage. Belling states that "the nodes which disappear between diplotene and late diakinesis do not seem to be all or mainly twists."

In a later paper Belling (1931) concludes that in the same species of *Lilium* the number of nodes is reduced from 42.5 at diplotene to about 30 at late diakinesis and metaphase, and suggests that the nodes which disappear are half-twists or temporary adhesions rather than chiasmata.

Darlington (1931 a) finds an average of 3.5 chiasmata at diplotene in *Primula sinensis* but only 1.89 chiasmata at metaphase. The bivalents at metaphase are associated only by terminal chiasmata. This decrease in number of chiasmata is attributed to terminalization.

Secale chromosomes at diplotene may often have four or five nodes, but never more than two at diakinesis and metaphase (Sax 1930).

In *Rosa blanda*, Erlanson (1931) obtains an average of 1.94 chiasmata per bivalent at early diakinesis, but only 1.31 at metaphase. Doubtless a greater number of chiasmata would have been found at diplotene.

In *Matthiola* Philp and Huskins (1931) found that the average chiasma frequency was 2.26 per chromosome at early diakinesis and only 1.54 at metaphase.

The counts of chiasma frequency at different stages of meiosis are summarized in Table 1. The estimated average crossover length of the chromosomes is calculated from the number of chiasmata which disappear between diplotene and metaphase on the basis of the writer's hypothesis. Since Belling considers that the chiasmata found at metaphase constitute all or most of the true chiasmata formed, the crossover length is also calculated on this basis. Darlington considers the nodes found at diplotene in *Primula* as chiasmata and attributes the loss of chiasmata to terminalization, so crossover lengths are also calculated on diplotene and early diakinesis counts.

TABLE 1

Genus	Ave. no. xta. per bivalent			Estimated Ave. c.o. length		
	Diplotene or early diakinesis	Metaphase	No. lost	S.	B.	D.
Tulipa.....	2.8	1.3	1.5	75	65	140
Lilium.....	3.5	2.5	1.0	50	125	175
Secale.....	3.5	1.8	1.7	85	90	175
Primula.....	3.5	1.9	1.6	80	95	175
Rosa.....	1.9	1.3	.6	30	65	95
Matthiola.....	2.3	1.5	.8	40	75	115
Callisia.....	4.2	1.5	2.7	135	75	210

Counts of chiasma frequency at early diakinesis do not represent the number formed at early diplotene so that in most of the genera listed above, the number of chiasmata lost should be increased considerably and consequently the crossover length would be increased on the writer's and on Darlington's hypotheses. Little is known concerning the crossover lengths of the chromosomes of the species listed above, but the calculated lengths are comparable to those found in *Drosophila* and *Zea*. Two of the autosomes in *Drosophila melanogaster* are somewhat more than 100 units long and in *Zea* the 5 chromosomes containing the most mutations range from about 50 to 68 units long (Lindstrom 1931). The chiasma frequency in *Zea* chromosomes is about 1.5 at metaphase (Randolph), but data on earlier stages are very meagre although Fisk (1927, Fig. 32) pictures two bivalents with about 5 nodes each. The genetic and cytological work on *Zea* should soon provide adequate data for a critical comparison of chromosome behavior and crossover frequency.

Darlington assumes that the reduction in number of chiasmata is due to terminalization. But as Belling (1931 b) points out, the coiling of the chromonemata would prevent any appreciable movement of the chiasmata after diakinesis. No coiled chromonemata have been described by Darlington, probably due to inadequate fixation or staining for showing this structure, rather than the absence of coiled chromonemata in the species studied. Coiled chromonemata have been described in many species and recently Shinke (1930) has described such chromosome structure in about 25 different genera. The coiling of the chromonemata probably begins at late diplotene so that no extensive movement of the chiasmata can occur, in most cases, between diplotene and metaphase. If it is assumed that the chiasmata are terminalized one might expect that all of them would frequently terminalize before metaphase and produce univalent chromosomes. In *Primula*, and in the *Solanaceae*, the bivalents at metaphase are usually associated only at the two ends forming the typical ring shaped bivalent. Darlington assumes that an average of about 1.5 chiasmata pass off the ends of the *Primula* bivalents. But why should the remaining two chiasmata always stop at the ends of the bivalent?

If each chiasma represents a crossover then the M chromosome of *Vicia faba* must be more than 400 crossover units long. Maeda (1930) finds an average of 8.1 chiasmata in this chromosome, and the number may be as high as 13 in some cases. On any theory of crossing over a twist must occur in the chromatids either at the chiasma or at an internode for every crossover. If one or more crossovers occur there should often be some interlocking of homologues at anaphase as seems to be the case in *Lilium* and *Lathyrus* (Maeda 1930, Sax 1930). With 8 crossovers one might expect considerable difficulty in separating homologues at the first meiotic division. If the chiasmata are not the result of crossovers there would of course be no difficulty in the division of homologues. (McClung 1927).

NON-DISJUNCTION AND CROSSING OVER.

Non-disjunction in *Drosophila melanogaster* was first described by Bridges in 1916. Primary non-disjunction is caused by the production of "2-X" and "no-X" eggs which when combined with normal sperm produce male and female exceptions. These primary exceptions occur with a frequency of about 1 in 2000. Male exceptions are usually produced from 4 to 8 times as frequently as female exceptions (Bridges 1916, Safr 1920, Mavor 1924, Anderson 1931). The excess of male exceptions, which are produced from

"no-X" eggs, is attributed to the failure of the XXs to pass to either pole at the first reduction division.

In normal stocks of *Drosophila* little if any crossing over takes place between the two X chromosomes which pass to the same egg. (Bridges 1916.) In high non-disjunction lines, crossing over is greatly reduced in both the normal and in the exceptional progeny (Morgan et al. 1925). In Anderson's (1929) high non-disjunction stock crossing over between scute and forked was reduced from 62 per cent to 20.9 per cent, and in the XXs which produced exceptional females the crossing over was only 7.3 per cent. Crossing over was almost eliminated in the region of vermillion, 40 units from the left end of the X, but increased towards the ends and was almost normal at the left end. Dr. Anderson informs me that the reduction in crossing over was caused by a translocation involving the X and the third chromosome. Dobzhansky (1932) also finds that translocations reduce crossing over and that non-disjunction is positively correlated with the length of the autosome attached to the Y. Due to the attraction of different chromosome segments chromosome pairing is often weak and crossing over is reduced.

In Anderson's (1931) primary exceptions produced by X-rays the total crossing over between scute and forked was about 60 per cent of the normal, but crossing over was found in all regions, and in two of the regions studied crossing over was almost normal. About 14 per cent of the XXs were homozygous for the forked locus where less than 5 per cent would be expected. This excess of homozygosis at forked is attributed to non-disjunction at the second maturation division, the only logical explanation of the results obtained. In view of the great irregularity of crossing over in different regions compared with the control it seems possible that there was 6 per cent of crossing over to the right of forked. At any rate crossing over between the XXs which pass to the same egg, is not confined to the distal ends of the chromosomes and some crossing over occurs to the right of forked.

In non-disjunction is due to a failure of XXs to separate at the first maturation division it is rather difficult to account for the decrease in crossing over in high non-disjunction stock if chiasmata represent crossovers. According to Darlington (1931) chiasmata form the only bonds between homologous chromosomes and if no chiasmata are formed the chromosomes would not be expected to form bivalents at meiosis. Failure of the XXs to disjoin would then be attributed to more than the usual number of chiasmata, but an excess of chiasmata would also mean an excess of crossing over on either Belling's or Darlington's interpretation. On the writer's

interpretation the decreased amount of crossing over in high non-disjunction lines could be attributed to few breaks at chiasmata so that the homologues would be united by more than the usual number of chiasmata and could not separate so readily.

There is good evidence, however, that non-disjunction is really a failure of chromosome pairing at the later stages of the first meiotic divisions. The decreased crossing over in high non-disjunction strains of *Drosophila*, and in the XXs which pass to the same egg in normal stock, can be attributed to non-conjugation or to pairing in only restricted regions of the chromosome. If only a few chiasmata are formed, due to incomplete pairing, then crossing over would be reduced on either theory of crossing over. The premature separation of homologues could be attributed to either early terminalization of these few chiasmata, or to breaks which would result in cross-overs. On Darlington's and Belling's theory, all of the chiasmata must be prematurely terminalized. The failure of chiasma formation, or breaks the few chiasmata formed, would produce unpaired homologues at the first maturation division. If these univalents pass at random to either pole, then half of the eggs should contain no X or 2 X chromosomes, and half should contain the usual 1 X. The univalents often fail to reach the poles in species hybrids and in haploids, and are often lost in the cytoplasm. If then one of the two X chromosomes should be lost there will be an excess of no-X eggs which produce the male exceptions. Such a behavior of the univalents would account for the excess of male as compared with female exceptions. This explanation of non-disjunction seems to be more plausible than the assumption that the two XXs are so intimately paired that they fail to divide and both pass to the same pole or fail to reach either pole.

If non-disjunction is due to a failure of the X chromosomes to separate it is difficult to account for the decrease in crossing over in high non-disjunction lines of *Drosophila* on the theories of crossing over proposed by Belling and by Darlington. On the other hand if non-disjunction is due to non-conjugation at metaphase, as seems probable, then all chiasmata must be broken or prematurely terminalized. If chiasmata are crossovers then all of the XX chromosomes which show crossing over must have separated prematurely by complete terminalization and elimination of all chiasmata. In the high non-disjunction stock of Anderson's about 7 per cent of the crossovers between the two XXs which pass to the same egg occur to the right of forked, and in the X-ray material 6 per cent of the crossovers may have occurred to the right of forked. In most of these forked equationals an additional crossover also occurs

to the left of forked. If crossovers produce chiasmata then in these chromosomes there are usually two chiasmata which must be terminalized to produce "non-disjunction" and one of the chiasmata is to the right of forked so that it would have to be prematurely terminalized for practically the entire crossover length of the chromosome. If such terminalization is possible it would seem that non-disjunction should be frequent, but primary exceptions occur with a frequency of about one in 2000, in normal stocks of *Drosophila*, and in only 2.5 per cent of the progeny from high non-disjunction lines. The cytological evidence also indicates that extensive terminalization or movement of chiasmata is improbable (Belling 1931 b).

If Painter's (1931) cytological map of the X chromosome is correct there is some possibility that premature terminalization could occur because the region from scute to forked constitutes only about a third of the cytological length of the X chromosome. Stern (1931) working with the same stock finds that the region from scute to forked constitutes about one-half of the X chromosome and his figures clearly support this interpretation. It would seem improbable that two chiasmata could be prematurely terminalized, one for more than half the length of the X chromosome. Even in species where the homologous chromosomes are always associated by only terminal chiasmata at metaphase there is little or no tendency for premature separation of the chromosomes.

On the writer's theory of crossing over it is not difficult to explain "non-disjunction" even where crossing over occurs near the spindle fiber end of the X chromosome. If few chiasmata are formed at diplotene and all of them break in certain bivalents, then these chromosomes will be loosely associated so that precocious disjunction before metaphase would be possible.

There are, however, certain types of double crossovers that are difficult to explain unless some terminalization of chiasmata occurs. In Anderson's high non-disjunction data there is 1 and in the X-ray data there are 4 double crossovers of the type $\frac{aab}{aba}$ or $\frac{bba}{bab}$. These reciprocal-equational double crossovers can only occur, on the writer's hypothesis, if there is an unbroken chiasma between sister chromatids between the first and second genetically detectable crossovers, or a twist in the sister chromatids between the second and third crossovers. In Anderson's (1931) table 3, one of these reciprocal-equational crossovers is the result of a second and third crossover since the forked locus is homozygous, but the other three double crossovers apparently involve a first and second crossover

because forked is heterozygous in these cases. Under such conditions it would be necessary to assume that a chiasma between sister chromatids must be prematurely terminalized to produce "non-disjunction." Since these chiasmata would be to the left of forked and in two cases to the left of cut, it is not impossible that premature terminalization might occur. It is also possible that these three reciprocal-equational crossovers are produced by second and third crossovers, and that the first crossover was a reciprocal to the right of forked, or that these exceptional crossovers are produced by the non-disjunction at the second maturation division.

The writer's hypothesis offers a simpler and more plausible explanation of "non-disjunction" than Janssen's partial chiasmotypy hypothesis, regardless of which interpretation of "non-disjunction" is correct.

RANDOM CROSSING OVER BETWEEN THE FOUR CHROMATIDS.

Crossing over is not limited to two of the four chromatids, because more than 50 per cent of the X and third chromosomes of *Drosophila* which emerge from the reduction division, have one or more crossovers. In 62 units of the X chromosome 54 per cent of the emerging chromosomes show at least one crossover (Anderson and Rhoades, 1931), and in the third chromosome 72.9 per cent of the chromosomes are crossovers (Redfield, 1930). If crossing over occurs only between the new chromatids as Belling (1931 a) has suggested, then not more than 50 per cent of the emerging chromosomes should be cross overs, regardless of the map length of the chromosome.

More recently Belling (1931 b) has assumed that "the old connecting fiber is indifferent as to which chromiole it will remain with." On this assumption crossing over would be at random between the four chromatids.

Belling's hypothesis can be modified to comply with certain cytological and genetic data. If the old connecting fibers usually remain with the old genes at the time the new chromatids are formed, then crossing over will usually occur between the two new chromatids as Belling (1931 a) has assumed. In some cases the old connecting fiber will unite a new and an old gene so that crossovers will occur between sister chromatids. Such crossovers, if sufficiently numerous, would result in random crossing over even if all crossovers at chiasmata were between the two new chromatids. Crossing over between sister chromatids would not be dependent on chromosome pairing and would be expected to occur with equal frequency in all regions of the chromosome.

On the writer's hypothesis random crossing over among the four chromatids can occur only if half-twists are sufficiently numerous in the paired sister chromatids. If the chromosomes are already split into sister chromatids at the time of meiotic pairing it would seem improbable that the same two non-sister chromatids would be paired throughout their length. If the secondary split occurs after pairing it would also be improbable that the sister chromatids would lie parallel throughout their length. One would expect some twists in the paired sister chromatids in either case. Such twists are found in both somatic and meiotic chromosomes.

In normal stocks of *Drosophila* and in cases of "non-disjunction," the genetic assortment of chromatids will be at random for the first crossover, because of their free assortment at the second maturation division. In attached-X stock, however, the random distribution at both first and second crossovers can be tested.

Random crossing over can occur in attached XXs, on the writer's theory, only if twists in paired sister chromatids are sufficiently numerous. Such half-twists could occur between the point of spindle fiber attachment and the first chiasma, or between the second and third chiasmata. (Diagram 10.) They could not occur between the first and second chiasmata without the formation of an additional chiasma between sister chromatids, but such chiasmata would be expected only in rare cases.

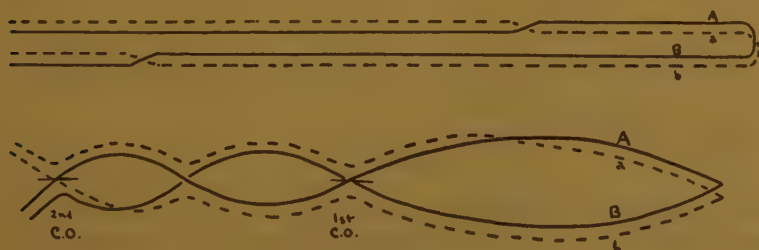


DIAGRAM 10

Only two types of first crossovers need be considered; (0) no twists in either pair of sister chromatids between the attachment point and the first crossover chiasma, and (1 a) one half twist in only one pair of sister chromatids, Aa. The other two types, (1 b) a half twist in chromatids Bb, or (1a-1b) in both pairs of sister chromatids, need not be considered since they are reciprocal to the first two types.

Between the first and second crossovers four types of chromatid association must be considered if crossing over is at random. There may be (0) no twists in either pair of sister chromatids, (1 a) one half-twist in chromatids Aa, (1 b) one half twist in chromatids Bb,

and (1a-1b) a half twist in each of the paired sister chromatids. If such half-twists are frequent there might be several of them between the point of attachment and the first crossover, or between crossovers, but if these twists occur at random they will produce the same types and proportions of crossovers as expected on the assumption that the above four types occur in equal proportions.

If no half twists occur as we would expect types (O) and (1a-1b) to be formed in equal proportions, but no types 1a or 1b would be expected. At a given chiasma crossing over could occur between A and b chromatids, or between B and a. If the first crossover is between A and b the second crossover may occur between A and b or between a and B. With no half twists in pairs of sister chromatids only equational crossovers could occur in attached XXs.

If chiasmata are produced by previous crossovers, the modification of Belling's hypothesis would seem to be the most plausible explanation of the mechanism involved. If sufficient crossovers occur between sister chromatids, the detectable crossovers will be at random between the four chromatids. The association of chromatids shown in diagram 11 will give the same random crossing over as direct crossing over between A and B or b, and B with either A or a.

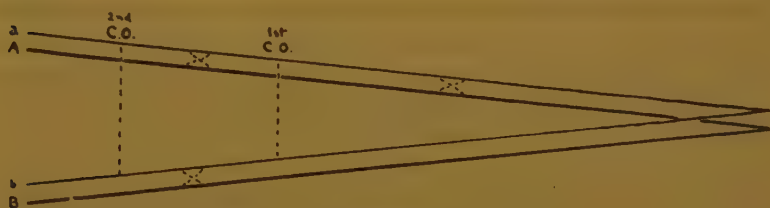


DIAGRAM 11

The detectable crossovers are shown by the lines connecting the two daughter chromatids. Only two types of chromatid association need be considered between the point of attachment of the X chromosomes and the first crossover;—(O) no crossovers occur in either pair of sister chromatids, and (1a) a sister crossover occurs in the Aa pair of chromatids. Between the first and second chiasmata there may be, (O) no sister crossovers, (1a) an excess of 1 sister crossover in chromatid Aa, (1b) an excess of 1 sister crossover in chromatid Bb, or (1a-1b) an equal number of sister crossovers in each of the pairs of sister chromatids.

On either theory we have 8 types of chromatid association in the attached X bivalents, which produce 16 classes of crossovers. The results of random crossing over at two points in the bivalent attached X chromosomes are shown in table 2.

TABLE 2

Types of chromatid association resulting from random crossing over at two points in attached X chromosomes.

C.O. Class	1st C.O. Sax	Bell.	2nd C.O. S. or B.	Crossover types	1st crossovers eq.	rec.	1	2	3	homozygosis 1st X ₁ a	2nd X ₁ a
1	0	1a	0	aaa — bab — bbb	2			2		2	
2	0	1a	1a	baa — aab — bbb	2			2		2	
3	0	1a	1b	aaa — bab — abb	2			2		2	
4	0	1a	1a, 1b	baa — aab — abb	2			2		2	
5	1a	0	0	aba — bab — bbb		1			1		
6	1a	0	1a	aba — aab — bbb	1	1	1				2
7	1a	0	1b	bba — bab — abb	1	1	1				2
8	1a	0	1a, 1b	bba — aab — abb		2					
					10	—	5	2	—	8	—
										8/16	4/16

In the second column are listed the types of first crossovers which have been considered on the writer's hypothesis and on the modified hypothesis of Belling. The genetic constitution of the attached XXs which pass to the egg cell are indicated under crossover types. Difference between chromatids A and a, or B and b, are not indicated since they cannot be detected by genetic tests. The first detectable crossovers from the attachment point are shown to occur in the ratio of 2 : 1 if crossing over is at random. Three types of second crossovers occur:—(1) equationals homozygous to the left $\left(\frac{ab}{aa} \text{ or } \frac{bb}{ba}\right)$, (2) equational crossovers homozygous to the right $\left(\frac{ab}{bb} \text{ or } \frac{aa}{ba}\right)$, or (3) reciprocal crossovers $\left(\frac{ab}{ba} \text{ or } \frac{ab}{ba}\right)$. With random crossing over these types should appear in the ratio of 2 : 8 : 1. At the left of the first crossover chiasma one-half of the attached X chromosomes should be homozygous, and one-fourth should be homozygous recessives. At the left of the second crossover chiasma one-fourth of the attached XXs should be homozygous and one-eighth recessives.

If crossing over is at random the first crossovers from the spindle fiber end in attached XX should be equationals and reciprocals in the proportion of 2 : 1 (Table 2). Anderson (1925) found equational and reciprocals in his attached X data, in the proportion of 29.7 to 15.6. Although there is a slight excess of equationals the ratio is very near random expectation. If equational and reciprocal first crossovers occur in the ratio of 2:1 then the percentage of homozygous recessives should be half of the crossover distance between the spindle fiber and the first crossover. For forked, which is about 10 units from the spindle fiber, the percentage of recessives in attached XXs was found to be 5.2 by Anderson, 4.9 by Rhoades, and 5.1 by Sturtevant. The genetic evidence indicates that the chromatids are assorted at random at the first crossover.

Random assortment of chromatids would be expected if there is an average of 0.5 or more half-twists or sister crossovers between the attachment point and the first crossover. Even with relatively few half-twists or sister chromatid crossovers in the X chromosome, random crossing over might be expected at the first crossover chiasma because the region between the spindle fiber and the first crossover would usually include more than half of the length of the chromosome (Stern 1931).

The randomness of chromatid association at the second crossover can be determined from the proportions of types of second crossovers in attached X and XXs from "non-disjunction." The non-

The data from Anderson and Rhoades (1931) table 1 have been used for the calculation of the frequency of chiasmata which produce

crossovers in the bivalent X chromosomes. Crossover recombinations are shown for 26,908 X-chromosomes of which 46 per cent showed no crossing over in the 62 units between forked and scute, 46 per cent were single crossovers, 7.6 per cent were double crossovers, 0.2 per cent were triple crossovers and .01 per cent were quadruple crossovers.

If crossing over is at random chiasma frequency can be obtained from crossover frequency as shown in table 5.

TABLE 5

Calculation of chiasma frequency based on crossover frequency in the X chromosome of *Drosophila*

	Number of crossovers per chromosome				
	0 46%	1 46%	2 7.6%	3 0.2%	4 .01%
-4th Xta.....	.01	.04	.06	.04	x16 = .16
	45.00	45.96	7.54	.16	
-3rd Xta.....	.16	.48	.48	x8 = 1.3	
	45.83	45.48	7.06		
-2d Xta.....	7.06	14.12	x4 = 28.2		
	38.77	31.36			
	31.36				
-1st Xta.....	8.41	x2 = 62.7			
Total chiasmata in bivalents.					
None	Single	Double	Triple	Quadruple	
8.4%	62.7%	28.2%	1.3%	.2%	

Since quadruple chiasmata, if crossing over is at random, should produce crossover chromatids in the proportion of 1 non-crossover, 4 singles, 6 doubles, 4 triples, and 1 quadruple, it is necessary to subtract proportional percentages from each class of crossovers, and repeat for triples, doubles, and singles in proper proportions. Only one chromatid in 16 produced by quadruple chiasmata (which produce crossovers) will be a quadruple crossover, so the percentage of quadruple crossovers must be multiplied by 16 to obtain the number of quadruple chiasmata. Similar calculations are used to obtain chiasmata frequency from single, double, and triple crossovers.

With the above frequency of single, double, and triple chiasmata it is possible to determine the percentage of homozygosis expected 62 units from the spindle fiber end of the two X chromosomes from attached X and non-disjunction stock. The percentage of homozy-

gosis at the left of the first crossover chiasma is 50, the second 25, (Table 2) and the third 37.5, if crossing over is at random. For homozygous recessives these percentages are 25, 12.5, and 18.75 respectively. The following table shows the percentage of homozygous recessives expected 62 units from the spindle fiber attachment in XX chromosomes.

Chiasmata =	Single	Double	Triple
	62.7%	28.2%	1.9%
% homo. recessives =	15.67%	3.52%	.24% = 19.4%

We would expect then, if crossing over is at random, to find 19.4 per cent of homozygous recessives in attached XXs at a point 62 units from the right end of the chromosome. The percentage of homozygosis found is significantly lower than expected. Sturtevant (1931) found 17.1 per cent homozygosis for scute, which is about 72 units from the right end of the X chromosome. This analysis was based on approximately 25,000 flies. Rhoades (1931) found about 18.6 per cent homozygosis for scute, but for ruby, which is about 64 units from the spindle fiber attachment, the percentage of homozygosis was found to be 17.7. Counts were made on about 42,000 flies. At a point 62 units from the spindle fiber the percentage of homozygosis recessives would be about 17.4 where 19.4 per cent would be expected on the basis of random crossing over.

Anderson's attached X data shows a similar discrepancy between the percentage of homozygosis found and the percentage expected on random crossing over. Chromosomes homozygous for the forked locus are assumed to have crossed over to the right of forked, and such chromatids are classed as crossovers in this region. Only one of the chromatids, equational at forked, is a crossover to the right of forked, but both are included to make up for the reciprocal crossovers to the right of forked which cannot be detected from the data. Considering these crossovers to the right of forked, there are 59.5 per cent of the chromatids with no crossovers, 37.2 per cent with one, and 3.3 per cent with two. In terms of crossover chiasmata, 25.6 per cent of the bivalent chromosomes have no chiasmata between the spindle fiber and end, 61.2 per cent have one chiasma, and 13.2 per cent have double chiasmata which break. If crossing over is at random the percentage of homozygosis for cut should be 16.5 per cent in the XX chromosomes listed in Anderson's table 6. The percentage of homozygosis actually found was 15.5, although for tan, still further to the right, the value was 16.1.

The percentage of homozygous recessives at the left end of attached X chromosomes is lower than expected if crossing over is at random. But, as Anderson and others have suggested, the

lower viability of the homozygous recessive segregates would reduce the percentage of these classes so that the true value might well approach the percentage expected on random assortment.

If there is any significant deficiency of homozygosis in attached X chromosomes, it would indicate that second cross-overs are not entirely at random. On the writer's hypothesis such a deficiency could be attributed to few half twists between the first and second cross over. For instance, if the average frequency of half twists were 0.25, the percentage of homozygous recessives 62 units from the fiber would be only 17.6 instead of 19.4 expected on random assortment. Belling's recent theory should always give random assortment for all cross overs. The modification of Belling's theory suggested by the writer would also fail to account for any deficiency of homozygous recessives. If crossing over is invariably at random between the four chromatids, Belling's theory would seem to be the most valid interpretation of the mechanism of crossing over. If, however, crossing over is not entirely at random, the writer's hypothesis seems to offer the only solution. Although there is a deficiency of homozygous segregates from attached X chromosomes, the nature of the genetic evidence does not justify any final conclusion concerning random assortment of the chromatids at the second cross over.

CHROMOSOME PAIRING AND CROSSING OVER.

When crossing over is eliminated in the *Drosophila* female there is also a loose association of homologous chromosomes. (Gowen 1922, 1928.) This behavior is undoubtedly analagous to the case of asynapsis in *Zea* (Beadle 1930). A decrease in crossing over may also be caused by inversions and translocations. Dr. Anderson informs me that his high non-disjunction line was caused by an inversion. In this case the decrease in crossing over was also associated with an increase in "non-disjunction" or failure of chromosome pairing. Dobzhansky (1931, 1932) has found that crossing over is decreased and non-disjunction increased in flies heterozygous for translocations. This behavior is attributed to conflicting attractions between homologous chromosome segments.

On either theory of crossing over the reduction or elimination of crossing over could be attributed to a differential rate of chromosome pairing compared with chromatid organization. At pachytene all four chromatids are associated, at diplotene only two chromatids can be associated and at telophase the two chromatids are united only at the spindle fiber constriction. If chromosome pairing is delayed then the sister chromatids might be at a stage commonly

found at diplotene, before the homologous chromosomes are paired, so that no chiasmata could be formed. In the cases of inversion no pairing of homologous genes would occur between inverted and normal chromosome segments and no crossovers could be produced in such regions. In heterozygous translocations chromosome pairing is delayed so that few chiasmata can be formed.

The genetic and cytological evidence shows that crossing over is most frequent at the distal end of the X chromosome (Painter, 1931) and at the distal ends of the third chromosome (Dobzhansky, 1930). This localization of crossing over would seem to indicate that chromosome pairing in *Drosophila* begins at the distal ends of the chromosomes and proceeds towards the spindle fiber. Crossing over would occur at the ends of the chromosomes because the chromatids are not sufficiently differentiated to prevent chiasma formation, but towards the spindle fiber the paired sister chromatids become so united that chiasma formation is no longer possible. Since chiasma formation is associated with crossing over, on either theory, there would be few crossovers in the spindle fiber region and frequent crossovers at the distal ends of the chromosomes.

Crossing over is increased in the X chromosome and in the autosomes of *Drosophila* by changes in temperature and by X-rays. (Plough 1917; Stern 1926; Muller 1925, 1926.) The increase in crossing over occurs primarily in the region of the spindle fiber attachment, but not in regions where crossing over is frequent in untreated flies. This behavior could be attributed to an acceleration of chromosome pairing so that in the region of the fiber attachment the chromosomes would be paired before the sister chromatids had sufficiently developed to prevent chiasma formation. Thus crossing over would be increased in the spindle fiber region of the chromosome.

Differences in types of chromosome association at meiosis might also be attributed to differences in the region where pairing begins. If pairing begins at the spindle fiber and proceeds slowly toward the ends, the chiasmata would be localized in the region of the fiber, as is the case in *Fritillaria* (Newton and Darlington, 1930). If pairing is completed before sister chromatids are sufficiently developed, then chiasmata will not be localized, but will be more or less uniformly distributed along the bivalent chromosome as is the case in *Lathyrus*, *Lilium* and *Vicia*. If pairing begins at the ends and proceeds slowly toward the middle, or if the sister chromatids develop rapidly, then the chiasmata will be terminal, as found in the Solanaceae.

Graubard (1932) has recently presented evidence, based on cross-

ing over in homologous chromosomes heterozygous for an inversion, which seems to indicate that pairing begins at the spindle fiber in the second chromosome of *Drosophila*.

SUMMARY.

A study of chromosome behavior at different stages of meiosis in a number of species of plants, together with an analysis of the genetic evidence in *Drosophila*, has provided some critical evidence in regard to the cytological mechanism of crossing over.

Janssen's partial chiasmotypy hypothesis has been supported by Darlington, Belling and Maeda, but it is shown that there is no critical evidence in favor of this theory. Belling has offered the only explanation of the mechanism of crossing over in connection with Janssen's hypothesis, but this explanation is not in accord with certain cytological and genetic evidence. Neither Belling's theory of crossing over nor Darlington's theory of meiosis can be reconciled with the cytological work of Robertson, Kaufmann and Sharp.

According to the writer's hypothesis crossing over is caused by breaks in two of the chromatids at a chiasma so that crossing over should be correlated with a reduction in the number of chiasmata between the diplotene and diakinesis stages of meiosis. In *Callisia repens* there is a considerable reduction in number of chiasmata per bivalent between the diplotene and metaphase stages. The work of other cytologists shows that the numbers of nodes or chiasmata are reduced during the prophases of meiosis in *Tulipa*, *Lilium*, *Primula*, *Rosa* and *Matthiola*.

The association of non-disjunction with a reduction in crossing over is apparently due to a weak association of homologous chromosomes in high non-disjunction lines of *Drosophila*. Where cross-overs occur in the X chromosomes which pass to the same egg cell the partial chiasmotypy hypothesis would necessitate premature terminalization of chiasmata, in some cases for practically the entire crossover length of the X chromosome. On the writer's hypothesis non-disjunction with crossing over is attributed to the formation of few chiasmata all of which are broken before diakinesis, resulting in a weak association of homologous chromosomes.

The ratio of different types of second crossovers and the percentage of homozygosis in attached X chromosomes in *Drosophila* suggests that the second crossover may not be at random between any two of the four chromatids. If crossing over is not random at the second crossover the writer's hypothesis will account for the deficiency of homozygosis. It is impossible to account for these

genetic results on Belling's hypothesis or on any logical modification of his hypothesis.

Localization of chiasmata and crossovers is attributed to the type of chromosome pairing and to the relation between chromosome pairing and chromatid development.

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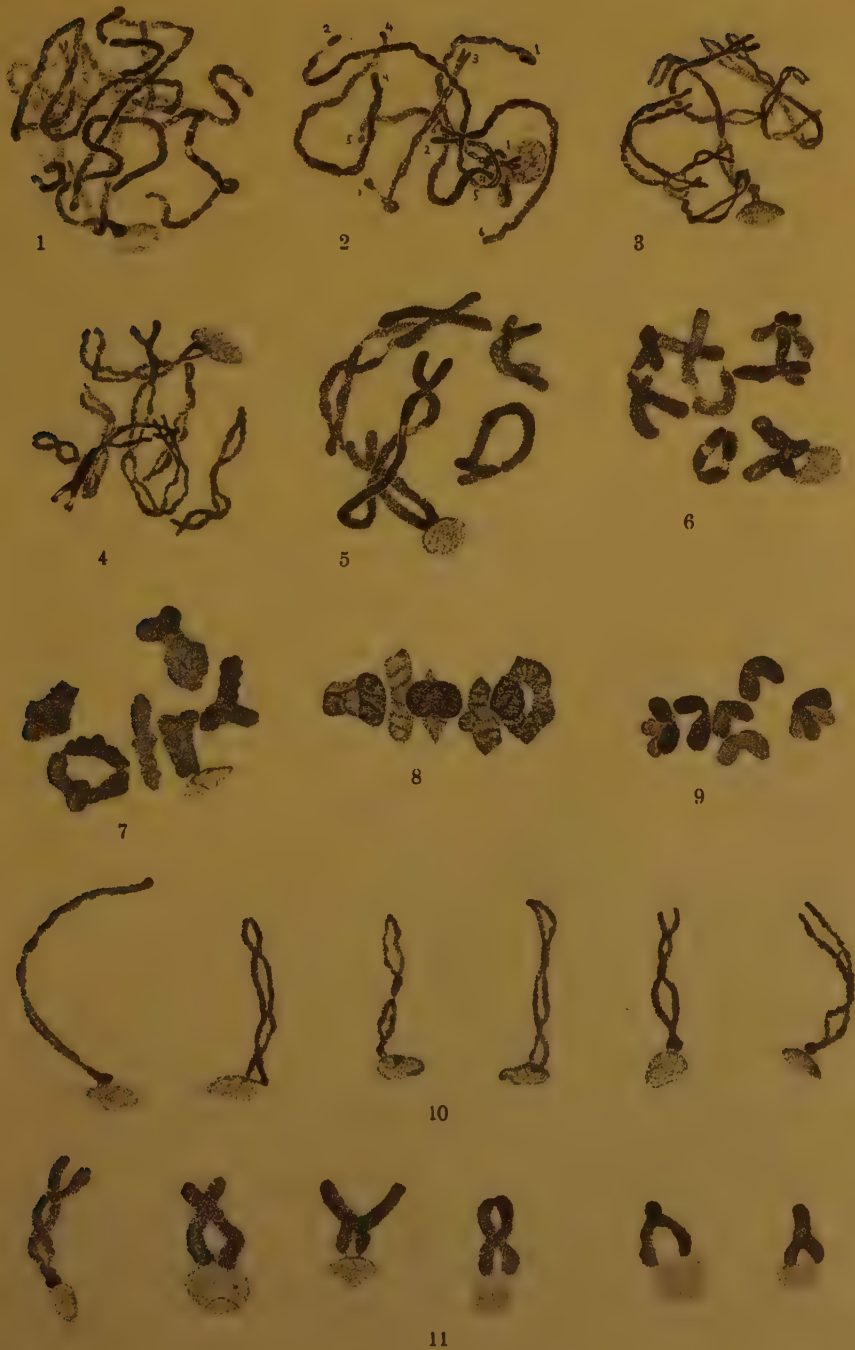
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DESCRIPTION OF PLATE 44.

Meiosis in the pollen mother cells of *Callisia repens*. Magnification $\times 3000$

- Figure 1. Pachytene stage. No continuous spireme observed at any stage in meiosis.
- Figure 2. Late pachytene. The six chromosomes can be observed more clearly at this stage. The nucleolus is always attached to one of the short bivalents.
- Figure 3. Early diplotene showing the chromosomes forming the nodes and internodes.
- Figure 4. Diplotene stage showing the number of nodes, most of which are probably chiasmata.
- Figure 5. Early diakinesis showing the reduction in number of nodes or chiasmata compared with the diplotene stage.
- Figures 6 and 7. Diakinesis. The nucleolus disappears between diakinesis and first metaphase.
- Figure 8. Metaphase of the first meiotic division. The chromosomes show the coiled chromonemata.
- Figure 9. Late anaphase showing spindle fiber attachment points. Two of the six chromosomes have a median attachment while four have terminal fiber attachments. Compare with text-figure 1.
- Figure 10. The nucleolus seems to be attached to the the same chromosome in all cases. This chromosome at late diplotene is shown at the left. Typical diplotene stages are shown in the other five chromosomes.
- Figure 11. The chromosome at the left is from a p. m. c. at early diakinesis. The other chromosomes show the number of chiasmata at diakinesis. Note the reduction in length of the bivalent from pachytene to diakinesis and the reduction in the number of nodes or chiasmata between diplotene and diakinesis.



MECHANISM OF CROSSING OVER

CONTRIBUTIONS TO THE TRADESCANTIA PROBLEM

EDGAR ANDERSON AND D. G. DIEHL

With plate 45 and three text figures

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INTRODUCTION

THE GENUS *Tradescantia* is as taxonomically difficult as it is cytologically superb. On the one hand its fugitive flower parts render herbarium specimens a poor record of the living plant; on the other those very phenomena (fragmentation, polyploidy, ring-formation) which attract the cytologist, produce intricate and puzzling relationships between species. It would remain a difficult genus to monograph if its floral characteristics were as well preserved in herbarium specimens as are those of the genus *Aster* for instance. Monographing *Tradescantia* from herbarium specimens alone would indeed be almost like working with a collection of *Compositae* from which the flowerheads had been removed.

Yet though the genus is an extraordinarily difficult one from the orthodox taxonomic viewpoint, it has much to recommend it for cyto-genetic studies. It grows easily from seeds or transplants and can withstand all sorts of mistreatment. It has a long-blooming period and artificial pollinations are not difficult to make. The chromosomes are enormous (they can sometimes be counted under low power) and are readily studied in smear preparations. Both tetraploid and diploid species and varieties occur in nature, and white, blue, and pink forms are already available for genetical analysis. It is by all odds one of the most promising native American genera for cyto-genetic investigations. Yet fundamental conclusions as to the evolutionary importance of cytogenetic phenomena will not be possible until they can be viewed against a background of sound morphological and taxonomical research.

If those geneticists and cytologists who are studying *Tradescantia*

would record, in addition to cytological details, the exact source of their material, and the nature of the pubescence on the leaves, on the sepals, and on the ovary, it would be possible to apply their findings to other problems besides those of chromosome structure.

TRADESCANTIA IN THE ST. LOUIS REGION

The following paper reports a preliminary cytological and genetical analysis of the *Tradescantias* of the Saint Louis region. It is a "report of progress" in an attempt to describe these species as they occur in that region, to evaluate the forces which have produced them, and to measure the evolutionary processes which are taking place within them at the present time.

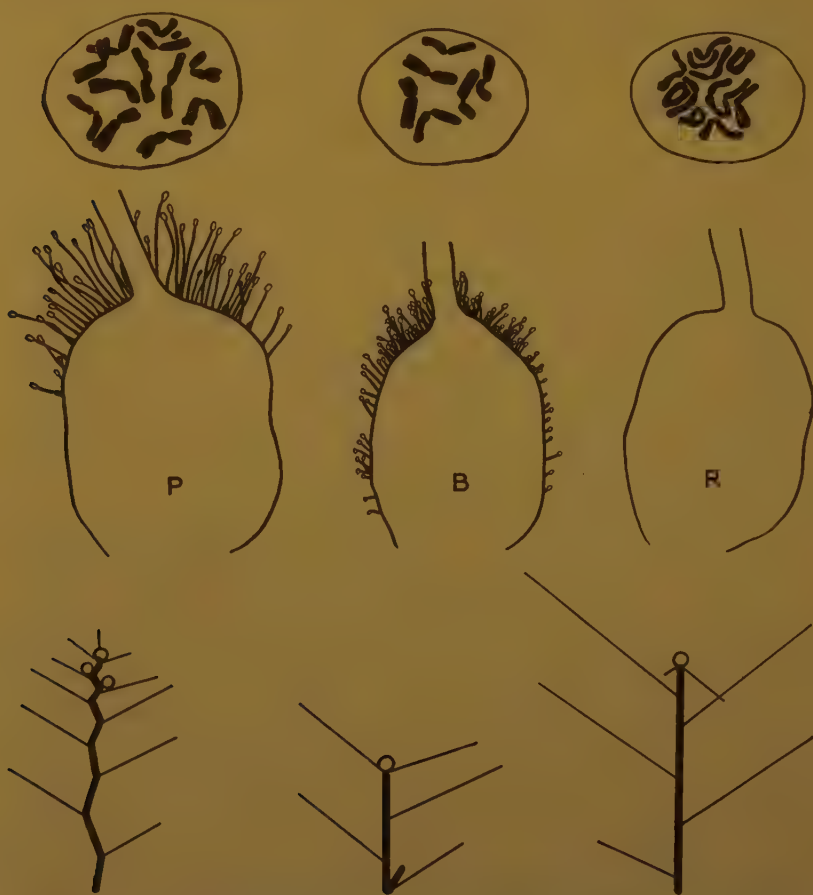


Figure 1. A comparison of the chromosome complement, the ovary, and the general habit of *T. pilosa* (left), *T. bracteata* (middle), and *T. reflexa* (right). Complete explanation in the text.

There are at least three species of *Tradescantia* in eastern Missouri. There may be more; there cannot possibly be fewer. If there eventually prove to be ten or twenty species they will even then fall into three groups. These three groups are separated from each other morphologically, ecologically, and cytologically. We are identifying them provisionally as *Tradescantia pilosa* Lehm., *T. reflexa* Raf., and *T. bracteata* Small. There are other *Tradescantias* in the state but we did not find them in the area covered by this study.

The outstanding differences between the three species are shown, somewhat diagrammatically, in figure 1. The middle row shows camera lucida drawings of the ovary and its pubescence. The lower row, reduced to scale from actual specimens, shows leaf size and number, length of node and number of nodes, etc. The upper row shows the gametic chromosome complement from camera lucida drawings of smears of pollen grain mitoses.

Tradescantia reflexa

Tradescantia reflexa is by far the commonest of the three species. It is tall and slender, glaucous throughout, with narrow, reflexed bracts. The ovary is completely glabrous or at most bears two or three tiny hairs at the base of the style. At Eureka, Missouri it was found on the limestone "glades" of the region. These are dry, stony hillsides with a semi-arid flora. They were apparently in this area the original home of the species, from which it has spread to railroad rights of way, dump-heaps, and the like. There was no apparent morphological or cytological difference between these "glade" populations and those along the railroad tracks.

Several of the colonies included variants, which had they not been connected with the normal type by a complete series of intermediates, might have been considered as taxonomically distinct. At Algonquin Station, Webster Groves, there were several very dwarf plants less than a foot high, but there were also a number of intermediates between these dwarfs and the rest of the colony. At Hamburg, Missouri, the opposite extreme was found, for several of the plants in this colony measured well over six feet in height. The most outstanding variation was seen at Hillsboro, Missouri, along a sandstone outcrop. The plants of this colony were all characterized by scattered hairs on the calyx in addition to the normal tuft usually found in *T. reflexa*. They were also differentiated by being early-flowering and it is possible that they are varietally distinct from the other plants of *T. reflexa* studied. For the present we have included them under *T. reflexa*. It is quite possible that they may be the result of hybridization with *T. bracteata*. In all of the above cases,

these peculiar forms were examined cytologically (both P M C and pollen divisions) and showed no divergences in chromosome numbers. Nineteen plants were recorded, as shown in Table 1. All were tetraploids ($2n = 24$). Many other plants were examined, and their chromosome numbers determined, but no definite record was made. Unfortunately the only plant showing a fragment chromosome was among these unrecorded individuals and it is not possible to say from which locality it came.

In spite of its variability, *T. reflexa* remains an easily recognizable unit over a very wide area. Colonies in south-western Michigan (Schoolcraft) and in southern Illinois (Ullin) seemed essentially the same as those examined in Missouri. The following collections available in herbaria represent plants morphologically similar to those we studied cytologically: *Lansing*, no. 3121, Mansfield, Mo.; *Lansing*, no. 3037, Cedar Gap, Mo.; *Ridgway*, no. 2116, Olney, Ill.

Examination of reduction divisions showed that *T. reflexa* was not only a tetraploid but was practically an auto-tetraploid. There was a very strong tendency for the chromosomes to conjugate in sets of four, the number of quadrivalents per PMC varying from 0 to 6. A count of ten PMC from a single smear of *T. reflexa* gave the following frequencies:

No. of times observed	No. of II's	No. of IV's
1	0	6
2	2	5
2	4	4
1	6	3
3	8	2
1	10	1

In the material examined the separation of quadrivalents was not at random. There was a very strong tendency (about 10 to 1) for adjacent chromosomes to pass to opposite poles. The data are consistent with the hypothesis that *T. reflexa* is an auto-tetraploid in which there is a slight differentiation between the two diploid sets of which it is made up. Its chromosome complement might be diagrammed as follows:

AA' BB' CC' DD' EE' FF'
AA' BB' CC' DD' EE' FF'

Tradescantia bracteata

As it occurs in Missouri this is a dwarf species seldom over a foot (3 dm.) in height. The ovary is covered with short glandular hairs (fig. 1). The flowering period is comparatively short and as the seed ripens the leaves die down and the plants pass through the summer in a semi-dormant condition. The flowers are more bril-

liant in color than those of *T. pilosa* or *T. reflexa*. Pink-flowered plants and blue-flowered plants are usually found growing together and albinos are not uncommon. The following collections represent material essentially similar to that which we studied cytologically: *Bush*, no. 684, Watson, Mo.; *Bush*, no. 336, Grandin, Mo.; *Davis*, no. 4403, Whiteside, Mo.

Tradescantia bracteata grows in abundance on rich black soil along roadsides and in wet meadows in the bottomland of the Mississippi River at Portage des Sioux, Missouri. The chromosome numbers of six plants from this locality were determined as is indicated in Table 1. All were diploids ($2n = 12$). One had a small fragment chromosome.

Tradescantia pilosa

This is by far the most distinct of the Missouri *Tradescantias*. In the St. Louis area it occurs only in shady situations, usually in rich sandy soil at the base of sandstone cliffs or in pockets on the face of the cliff. Since sandstone areas in eastern Missouri are mainly confined to a long narrow outcrop of St. Peter sandstone, *T. pilosa* is an uncommon species there. It was found in abundance

TABLE 1

Chromosome Numbers of wild-growing *Tradescantias* from eastern Missouri.
(Including a few plants of *T. reflexa* from outside that region.)

SOURCE	P M C	POLLEN GRAIN MITOSIS
<i>T. reflexa</i>		
Hillsboro, Mo.....	$n = 12$	—
Hillsboro, Mo.....	—	$n = 12$
South Webster, Mo.....	—	$n = 12$
Eureka, Mo.....	$n = 12$	$n = 12$
Hamburg, Mo.....	—	$n = 12$
Hamburg, Mo.....	—	$n = 12$
? , Mo.....	—	$n = 12 + f$
Antonio, Mo.....	—	$n = 12$
Ullin, Ill.....	—	$n = 12$
Ullin, Ill.....	—	$n = 12$
Ullin, Ill.....	—	$n = 12$
Ullin, Ill.....	—	$n = 12$
La Crosse, Wis.....	—	$n = 12$
Schoolcraft, Mich.....	$n = 12$	$n = 12$
Schoolcraft, Mich.....	—	$n = 12$
Schoolcraft, Mich.....	—	$n = 12$
Schoolcraft, Mich.....	—	$n = 12$
<i>T. pilosa</i>		
Hermann, Mo.....	$n = 12$	—
Hermann, Mo.....	—	$n = 12 + f$
Marthasville, Mo.....	$n = 12$	—
Marthasville, Mo.....	—	$n = 12$
<i>T. bracteata</i>		
Portage des Sioux, Mo.....	$n = 6$	$n = 6$
Portage des Sioux, Mo.....	—	$n = 6 + f$
Portage des Sioux, Mo.....	—	$n = 6$
Portage des Sioux, Mo.....	—	$n = 6$
Portage des Sioux, Mo.....	—	$n = 6$
Portage des Sioux, Mo.....	—	$n = 6$

at Marthasville, Hermann, Ashland, and Winfield, Mo. The following collections, available in many of the larger herbaria, represent material essentially similar to that which we studied cytologically: *Eggert*, St. Louis, Mo.; *Davis*, no. 3604, Hannibal, Missouri; *Eggert*, Hematite, Mo.; *Palmer*, no. 34,802, Pontiac, Missouri.

In general aspect *T. pilosa* is entirely different from any other Missouri Tradescantia. The stem is tall and zig-zag, the entire plant is sparingly pilose. The flowering season is late (July to August). The ovary bears long scattered hairs with relatively small glands at their tips. (Fig. 1). The chromosome numbers of 4 plants were determined; as reported in Table 1. All were tetraploids ($2n = 24$).

A COMPARISON OF VARIATION IN DIPLOID AND TETRAPLOID SPECIES

As has been reported above, *T. reflexa* (in Missouri, Illinois, Wisconsin, and western Michigan) was found to be a tetraploid species. *T. bracteata*, on the other hand, was a diploid. That is, *T. bracteata* like most normal animals and plants had its chromosomes in sets of twos. Those of *T. reflexa* on the other hand, were in sets of fours. This tetraploid condition should have a very marked effect upon the nature of individual differences in the two species. It should increase not only the proportion of intermediates but the number of intermediate types. An example may make this more clear.

Let us consider the simplest possible case, a single factor difference, albinism, for example, as it might be expected to operate in the diploid *T. bracteata*, on the one hand, and in the tetraploid, *T. reflexa* on the other. The inheritance of albinism in Tradescantia, so far as we know, has not actually been studied but the circumstantial evidence from forms existing in nature is all in accord with the hypothesis that as in practically all other flowering plants it is due to a single recessive gene. If we represent the gene for albinism by *a*, and its normal allelomorph by *A*, an albino plant of *T. bracteata* will be of the genetical composition (*aa*) and a pure-breeding full-colored plant will be (*AA*). Crossing the two will give us a heterozygous F_1 (*Aa*) which, selfed or crossed *inter se*, will produce the familiar $\frac{1}{4}$ (*AA*) $\frac{1}{2}$ (*Aa*) $\frac{1}{4}$ (*aa*) in the second generation. That is, in the diploid species, as regards the gene for albinism, there can be only three possible genetic types, the pure albino (*aa*) the pure-breeding normal (*AA*) and the heterozygote (*Aa*).

In the tetraploid *T. reflexa*, on the other hand, a pure albino must have a gene for albinism in each of the four sets of chromosomes and will be of the genetic constitution (*aaaa*). A cross with a homozygous (true-breeding) full-colored individual (*AAAA*) will in the

second generation produce full-colored (AAAA), albinos (aaaa), and three genetically different types of intermediates (AAAa), (AAaa), and (Aaaa). Whereas, in the diploid there were only three possible genetic types, there will be five in the tetraploid.

TABLE 2
A comparison of a cross between albinism and color in a diploid and an autotetraploid.

	DIPLOID	TETRAPLOID
Color parent.....	AA	AAAA
Albino parent.....	aa	aaaa
First generation.....	Aa	AAaa
Second generation.....	AA....25%	AAAA.... 2.8%
	Aa....50%	AAAa....22.2%
	aa....25%	AAaa....50.0%
		Aaaa....22.8%
		aaaa..... 2.8%

The differences between the two examples are set out diagrammatically in Table 2. It will be seen that in the tetraploid second generation as compared with the diploid, there are (1) three kinds of intermediates instead of one, (2) a much higher proportion of intermediates (94% instead of 50%). This will result in the tetraploid being tremendously more variable (using the word in its biological sense). In our hypothetical case of albinism in a population breeding at random and with, as is usually the case, the full-colored forms somewhat more variable than the albinos, we may expect in the diploid a large number of dark blues (AA), a large number of intermediates (Aa) and a few whites (aa). With exactly the same premises we will find in the tetraploids, very few dark blues and a large proportion of intermediates of various shades of blue and a very few pure albinos or none at all.

The same situation which has been outlined for albinism will apply to all the other genes; all will be present in sets of four instead of in sets of two. The change from pink flower to blue flower is apparently mainly due to a single factor. In a population of *T. bracteata* segregating for albinism and for pink we would expect to find only light and dark pink, light and dark blue, and white. In a similar population of *T. reflexa* we might expect to find blues, various intermediate magentas, and perhaps a few pinks, all in many degrees of color intensity.

These hypothetical deductions (which had been worked out from greenhouse material before we examined wild populations) are interesting because they agree exactly with what we actually *did* find. Large populations of *T. reflexa* were studied at five localities and *T. bracteata* was studied at two widely separated ones. The

data are summarized in Table 3. Those on flower color are difficult to present because of the variability of the tetraploids. In the diploid *T. bracteata* it was a simple matter to score the flowers as either pink or blue. Among the plants of *T. reflexa* any attempt at classification (aside from the extremely rare pure pinks) was extremely difficult and frankly artificial. In Table 3 an attempt is made to record the prevailing color types in each colony and the actual number of pure pinks or pure albinos. In another section of this paper one colony is taken up in as great detail as possible. The variation there reported is typical.

The number of genes segregating in a wild population is probably to be numbered by the thousands. For each of these the same situation will prevail which has been outlined in detail for those for pink and for albinism. The net result will be a tremendous increase in the total possible number of genotypes in each population, and in the number and proportion of intermediates. Nearly every taxonomist who has worked with *T. reflexa* has commented on its peculiar variability. While the fact that it is a tetraploid (and practically an auto-tetraploid) does not explain all the peculiarities met with in this species, it is responsible for many of them.

Students of the group have commented on the fact that some species of *Tradescantia* customarily produce both pink-flowered and blue-flowered plants, while other species do not. Rose (1899) for instance, has included this characteristic in forming his specific descriptions. The cytological and genetical data reported above provide a logical explanation for this interesting difference.

TABLE 3

Variation in flower color in populations of *T. reflexa* and *T. bracteata*.

SPECIES	LOCALITY	PREVAILING FLOWER COLORS	NO. OF PURE PINKS	NO. OF PURE WHITES
<i>T. reflexa</i>	Algonquin, Webster Groves, Missouri	Blue, blue-magenta, magenta, magenta-pink	1	0
<i>T. reflexa</i>	S. Webster, Missouri	Blue, magenta-blue, magenta-pink	0	0
<i>T. reflexa</i>	Hamburg, Missouri	Dark-blue, blue, blue- magenta	0	0
<i>T. reflexa</i>	Hillsboro, Missouri	Dark-blue, blue	0	0
<i>T. reflexa</i>	Ullin, Illinois	Dark-blue, magenta, magenta-pink	0	0
<i>T. reflexa</i>	Schoolcraft, Mich.	Dark-blue, grey-blue, deep magenta, pale magenta	0	0
<i>T. bracteata</i> . . .	Portage des Sioux, Mo.	Bright blue 39, blue- magenta 1	14	0
<i>T. bracteata</i> . . .	Tama, Iowa	Blue 1100 ±	380 ±	6

VEGETATIVE REPRODUCTION IN TRADESCANTIA

Throughout his paper on the Tradescantiae, Darlington (1929) has assumed that *T. virginiana*¹ is propagated mainly, if not entirely, by vegetative means. He presents no experimental evidence for this conclusion other than to describe the cytological conditions which according to his theories make vegetative propagation obligatory. The following quotations are representative of his point of view: p. 254. "The fact that we have forms of *Tradescantia virginiana* with fragments that do not answer to the requirements of meiosis merely *emphasizes the unimportance of sexual reproduction in preserving this species.*"

P. 254. "*T. virginiana* itself has drifted into an evolutionary back water in which *vegetative propagation has become excessively important.*

P. 278. "In *Tradescantia crassifolia* and *T. bracteata*, however, the various abnormalities must *reduce seed-production to negligible proportions if they reproduce themselves normally.*"

P. 279. "More recently Bush (1904) for example, has distinguished 18 different species from Texas alone; these would probably all resemble the types described cytologically [They do not. The seven that we have examined so far have been diploids.] and would be interfertile so far as they were fertile at all. It need hardly be said that none of them would be consistently true-breeding."

As will be demonstrated below this very logical theory is completely erroneous. We have not found the slightest scrap of evidence to support the thesis that tetraploid Tradescantias like *T. virginiana* and *T. reflexa* are dependent upon vegetative propagation. On the other hand we have found abundant evidence that it is even less highly developed among them than among the simple diploids from which they probably arose. Darlington's erroneous conclusions are probably due in part to his ignorance of the fact that these species are usually self-sterile.² Isolated specimens in gardens or greenhouses cannot be made to set seed. Moore (1917) had previously reported the fact, and we have been unable to obtain seed from self-pollination of any of the plants we have under cultivation, though they set seed readily in cross-pollinations.

There are two ways in which Darlington's hypothesis can be tested. We have evidence on both points.

¹ It should be remembered that Darlington includes not only the closely related species *T. reflexa*, but also the southwestern low-growing species *T. bracteata*, *T. humilis*, etc., as varieties and sub-species of "*T. virginiana* L. (U. S. A.)."

² On p. 272 and again on p. 274 he uses the hypothesis of "*continued self-fertilization*" to explain his results.

I. SEED PRODUCTION.

Prolonged search during the fruiting season failed to reveal a plant which was not producing seeds. No doubt such plants do exist, but none was found among the several hundred we examined. Most of the plants we examined were setting abundant seeds and many of the populations included young seedling plants.

II. VARIABILITY BETWEEN PLANTS IN WILD POPULATIONS.

The morphological consequences of vegetative and sexual reproduction are so different that a careful morphological analysis of wild populations will yield critical evidence. Such an analysis will do more than demonstrate merely the occurrence or non-occurrence of vegetative reproduction. It will make possible an evaluation of the relative importance of sexual and vegetative reproduction in maintaining the species. If vegetative reproduction is of any considerable importance its existence will be demonstrated in three different ways:

(1) The persistence of an actual organic connection between the parent plant and its vegetatively derived offspring.

(2) the frequent occurrence of morphologically indistinguishable plants which had originated vegetatively from a single individual, but in which the connection had died out or had been severed.

(3) The occasional appearance of a single, isolated individual.

These are all probably self-evident, except perhaps (3) which follows from the fact that if a species reproduces actively from seeds as well as by vegetative means, a single individual introduced into a virgin locality will soon be surrounded by seedlings, which will vary among themselves.

It would not have been surprising to have found any or all of these conditions in *Tradescantia* since all three are commonly met with among the Monocotyledons. An entire meadow is occasionally colonized by a single clone of *Iris* nor is it uncommon in that genus to find neighboring plants with no remaining evidence of an actual physical connection, between whose flowers there are no greater differences than exist on either plants. On all three of these points, however, we have evidence that vegetative reproduction is of minor importance in the tetraploid *T. reflexa*.

(1) Among the plants of *T. reflexa* which we studied there was never the slightest evidence of an organic connection between neighboring plants. Spreading by rhizomes was limited to a compact area around the parent stem.

(2) In not a single instance did we find two neighboring plants which could not be easily distinguished (see Table 4 and text fig. 2). Transplant experiments with a few of these types showed



Figure 2. A belt transect of eight two-meter quadrats at Algonquin, Missouri. Each circle represents a single clone and the area is roughly that of the crown at the time of flowering. Unshaded plants bore blue flowers, diagonal lines represent blue-magenta flowers, cross-hatching magenta, and solid black represents pink. Further description of the plants in Table 4. The divisions of the scale represent five feet.

that these individual differences were largely inherent and persisted under cultivation.

(3) We never found an isolated clone of *T. reflexa*. In every case if there was one plant there were from a dozen to several thousand other plants nearby. Although a clone of *T. reflexa* will persist for years under cultivation, gradually increasing in size, the largest we found in nature had a crown under three feet in diameter, and the crowns of the majority of wild plants are less than six inches across. As a matter of fact, the diploid species *T. bracteata* is more vegetatively vigorous than its tetraploid relative and often produces clones over two feet in diameter.

A DETAILED STUDY OF ONE COLONY OF *T. REFLEXA*

A typical colony of *T. reflexa* was chosen for intensive study and a part of the data collected are presented in Table 4 and figure 2. The colony occupied two or three acres along the Missouri Pacific right of way near the Algonquin suburban station in Webster Groves, Missouri. Eight two-meter quadrats were laid out in one belt transect. The individual clones were scored for height, pubescence of sepals and ovary, flower color, and number of stems.

While the variation in flower color and in pubescence was somewhat greater than we usually found, it was by no means exceptional. The variation in height of stem and size of clone was, on the other hand, less extreme than the average. The seed capsules of *Tradescantia* explode when ripe and discharge their seeds over a radius of a few feet. If a colony is left undisturbed there would soon be a tendency for seedlings to show greater resemblances to neighboring plants than to the colony as a whole. There is some circumstantial evidence from this colony and from other colonies that in this way seedlings tend to grow up around a prolific mother plant and form small "neighborhoods" in which adjacent plants resemble one another more closely than they do the colony at large. It will be seen from figure 2 that plants of different colors are not distributed at random. This was even more evident when the whole colony was examined. Although no two neighboring plants were identical there was often a "family resemblance" between them, and pink and magenta flowered plants tended to occur in groups.

A SURVEY OF SOUTHWESTERN TRADESCANTIAS

In addition to the material which we collected personally we were enabled through the kindness of Dr. B. C. Tharp of the University of Texas and Dr. D. W. Moore of the University of Arkansas to make a preliminary survey of the *Tradescantias* from those regions.

TABLE 4

CLONE	HEIGHT OF STEM	PUBESCENCE ON		FLOWER COLOR (APPROXIMATE)	No. OF STEMS
		SEPALs	OVARY		
AA	short	tufted at apex	glabrous	medium magenta	UNLESS OTHERWISE INDICATED THERE WAS ONE STEM PER CLONE
AB	short	scattered	glabrous	medium magenta	
AC	short	scattered	a few hairs at base of style	medium magenta	
AD	medium	tuft at apex	glabrous	medium magenta	
AE	medium	scattered	hairs at base of style	medium blue	
AF	short	scattered	glabrous	blue	
AG	medium	scattered	glabrous	blue	
AH	medium	scattered	hairs at base of style	magenta	
AI	medium	tuft at apex	glabrous	blue	
AJ	medium	lightly scattered	glabrous	blue	
AK	medium	lightly scattered	glabrous	medium magenta	three stems
AL	medium	lightly scattered	glabrous	dark blue	
AM	medium	lightly scattered	glabrous	dark blue	
AN	medium	lightly scattered	glabrous	dark blue	
AO	medium	lightly scattered	glabrous	dark blue	
AP	medium	lightly scattered	glabrous	medium magenta	
AQ	medium	lightly scattered	glabrous	blue	
AR	medium	lightly scattered	glabrous	medium magenta	
AS	short	lightly scattered	glabrous	blue	
AT	medium	lightly scattered	glabrous	medium magenta	
AU	tall	tuft at apex	glabrous	blue	
AV	medium	tuft at apex	glabrous	medium magenta	
AW	medium	tuft at apex	glabrous	blue	
AX	medium	tuft at apex	glabrous	medium magenta	
AY	short	scattered	glabrous	medium magenta	
AZ	tall	scattered	glabrous	medium magenta	
BA	tall	tuft at apex	glabrous	blue	
BB	medium	tuft at apex	glabrous	blue	
BC	short	scattered	glabrous	blue	
BD	short	scattered	glabrous	medium magenta	
BE	past blooming				
BF	medium	scattered	glabrous	medium magenta	
BG	medium	tuft at apex	glabrous	medium magenta	
BH	tall	tuft at apex	glabrous	medium magenta	
BI	medium	lightly scattered	hairs at base of style	light blue	
BJ	medium	tuft at apex	hairs at base of style	medium magenta	
BK	medium	tuft at apex	glabrous	medium blue	
BL	short	scattered	glabrous	blue	
BM	medium	scattered	glabrous	medium magenta	
BN	medium	scattered	glabrous	medium magenta	
BO	medium	scattered	glabrous	medium magenta	two stems
BP	medium	scattered	glabrous	blue	
BQ	medium	scattered	glabrous	blue	
BR	medium	tuft at apex	glabrous	magenta	
BS	medium	tuft at apex	glabrous	magenta	
BT	medium	tuft at apex	glabrous	medium magenta	
BU	short	scattered	glabrous	medium magenta	
BV	medium	scattered	glabrous	medium magenta	
BW	medium	scattered	glabrous	blue	
BX	medium	tuft at apex	glabrous	magenta	
BY	medium		through blooming		two stems
BZ	tall	scattered	glabrous	blue magenta	
CA			Seedling		
CB	tall	scattered	glabrous	medium magenta	

TABLE 4—Continued

CLONE	HEIGHT OF STEM	PUBESCENCE ON		FLOWER COLOR (APPROXIMATE)	No. OF STEMS
		SEPALs	OVARY		
CC	tall	scattered	glabrous	dark blue	four stems
CD	medium	scattered	glabrous	dark blue magenta	
CE	medium	tuft at apex	glabrous	medium magenta	
CF	short	tuft at apex	hairs at base of style	pink	
CG	medium	tuft at apex	glabrous	blue	
CH	medium	scattered	glabrous	dark blue	
CI	tall	tuft at apex	glabrous	dark blue	two stems
CJ	tall	tuft at apex	glabrous	dark blue	two stems
CK	medium	scattered	glabrous	light blue	
CL	tall	tuft at apex	glabrous	dark blue magenta	three stems
CM	short	tuft at apex	glabrous	blue	
CN	short	tuft at apex	glabrous	dark blue magenta	two stems
CO	tall	tuft at apex	glabrous	dark blue	
CP	medium	scattered	glabrous	dark blue	
CQ	tall	scattered	glabrous	dark blue	three stems
CR	medium	tuft at apex	glabrous	dark blue	seven stems
CS	medium	scattered	glabrous	blue	four stems
CT	short	scattered	glabrous	magenta	
CU			Seedling		
CV	short	scattered	glabrous	blue	
CW	medium	tuft at apex	glabrous	blue	
CX	short	tuft at apex	glabrous	magenta	
CY	medium	scattered	glabrous	blue	seven stems
CZ	medium	scattered	glabrous	blue	
DA	medium	scattered	glabrous	dark magenta	
DB	short	tuft at apex	glabrous	light blue	
DC	tall	tuft at apex	glabrous	blue	
DD	tall	tuft at apex	glabrous	medium blue	large clone
DE	medium	scattered	glabrous	blue	
DF	short	scattered	glabrous	blue magenta	
DG	short	tuft at apex	glabrous	blue magenta	
DH	short	tuft at apex	glabrous	blue magenta	
DI	tall	scattered	glabrous	light blue	large clone
DJ					
DK	medium	scattered	glabrous	blue magenta	
DL	medium	scattered	glabrous	dark blue	large clone
DM	tall	tuft at apex	glabrous	light blue	large clone
DN	tall	tuft at apex	glabrous	dark blue	five stems
DO	medium	scattered	glabrous	magenta blue	four stems
DP	tall	scattered	glabrous	blue	large clone
DQ	medium	tuft at apex	glabrous	blue	
DR	medium	scattered	glabrous	blue	
DS	medium	scattered	glabrous	magenta	
DT	tall	scattered	glabrous	medium blue	seven stems
DU	medium	scattered	glabrous	light blue	

The material was forwarded just before it came into bud and was grown in the greenhouse, where material for smears was obtained. The following species were examined: (with the exception of *T. texana* the determinations are those made by Dr. Tharp.)

	P M C	POLLEN MITOSIS
<i>T. humilis</i>		
plant A.....	n = 6	—
plant B.....	n = 6 + f	n = 6 + f
<i>T. edwardsiana</i> ¹	—	n = 6

¹ *Tradescantia edwardsiana* Tharp in *Rhodora*, xxxiv. 57, fig. 1 (1932).

	P M C	POLLEN MITOSIS
<i>T. hirsuticaulis</i>	—	n = 6
<i>T. texana</i>	n = 6	n = 6
<i>T. gigantea</i>		
plant X.....	n = 6 + f	n = 6 + f
plant Y.....	n = 6	n = 6
<i>T. occidentalis</i>	—	n = 6
<i>T. sp. (reflexa ?)</i> from Texas.....	—	n = 6
<i>T. sp. (reflexa ?)</i> from Arkansas.....	—	n = 6

It will be noticed that whereas two of the species in the St. Louis region were tetraploids, all of the material from the southwest was diploid. One of the species from Texas and all of the plants from Arkansas were very similar to *T. reflexa* as it occurs in Missouri; just how similar could not be determined since the southern material was forced into bloom under abnormal conditions. If these plants do not belong to *T. reflexa*, they must certainly form a very closely related species. Since the Missouri and other northern material of *T. reflexa* was all tetraploid it is therefore quite possible that polyploidy is intraspecific in *Tradescantia* and that diploid and tetraploid races may occur within the same species.



Figure 3. Ovaries of six species of *Tradescantia* from the neighborhood of Austin, Texas. Drawn, greatly enlarged, with camera lucida. From left to right: G; *T. gigantea*; E; *T. edwardsiana*; R; *T. reflexa*; T, *T. texana*; H, *T. hirsuticaulis*; O, *T. occidentalis*.

It is particularly interesting that the tetraploid *Tradescantias* should be more northerly than the diploids. Sax (1931) has reported in the closely related genus *Rhoeo*, the artificial production of tetraploids by exposure to low temperatures. A similar geographical position for tetraploid races and species to the north of their diploid relatives has been reported for a number of genera. Hagerup (1928) collected six such cases in the *Bicornes* alone and has recently summarized the evidence on polyploid geographical races (1932). It is particularly interesting that Mangelsdorf and Reeves (1931) working with another American monocot of tropical affiliations (*Tripsacum dactyloides*) have found that the plants collected in Texas are diploids while those from the north and east are tetraploids.

It may be well in passing to point out that the differences between the seven diploid species from Texas are quite as great, on the whole, as are those between the three Missouri species. Polyploidy here, as elsewhere, has introduced complexity into inter-specific relationships, but species differentiation has taken place to an even greater extent in regions where polyploidy was absent.

Table 5 summarizes the outstanding differences between these species. Camera lucida outlines of their ovaries are shown in figure 3. While instances of inter-specific hybridization are not unknown, most of these Texas species are kept apart by habitat differences and maintain themselves as recognizable units over a wide area.

TABLE 5—A TABULAR COMPARISON OF SPECIES DIFFERENCES IN TEXAS AND MISSOURI

SPECIES	STEM	FLORAL LEAVES	PUBESCENCE ON		
			LEAVES	SEPALS	OVARY
TEXAS SPECIES:					
<i>T. texana</i>	short, weak branched	long, equal	long, vil-lous	dense, glandular	a few glandular hairs at top
<i>T. gigantea</i>	tall	short, sub-equal, dense-ly pilose	glabrous	dense, non-glandular	very dense, non-glandular
<i>T. hirsuticaulis</i>	tall	short, unequal	hirsute	sub-gland-ular	glandular and non-glandular
<i>T. humilis</i>	short	unequal	hirsute	glandular	dense, gland-ular
<i>T. occidentalis</i>	slender	slender	glabrous	scattered glandular	glandular and non-glandular
<i>T. sp. (reflexa ?)</i>	medium	long, unequal	glabrous	glabrous except for tuft at apex	glabrous
MISSOURI SPECIES:					
<i>T. reflexa</i>	medium to tall	long, unequal	glabrous	glabrous except for tuft	glabrous
<i>T. bracteata</i>	short	very long, subequal	scattered, glandular	glandular	dense, glandular
<i>T. pilosa</i>	tall zig-zag	sub-equal	scattered, pilose	glandular pilose	scattered, glandular

CONCLUSIONS

It should be remembered that the following conclusions are little more than working hypotheses and that they are put forward tentatively at the end of our first year of intensive work. In beginning this study we had as our objectives (I) the description of the species of *Tradescantia* as they occur in nature and (II) the evaluation of the evolutionary processes which are taking place in them at the present time.

I. As regards the description of these species and their separation and classification we feel that they are a difficult group but by no means an impossible one. Their inter-specific relationships are not nearly so intricate as are those of such genera as *Rubus* and *Crataegus*, for instance. In this connection we have found the pubescence on the ovary a particularly useful character because it varies so little within species. A colony of *Tradescantias* may vary strikingly in size and general aspect from plant to plant and yet the pubescence on the ovary will be the same throughout the colony. The pubescence also varies widely from species to species. It may be dense, or sparse, or restricted to one part of the ovary, or completely wanting. The hairs may be long or short, and glandular or non-glandular. Used in connection with other characters it is very helpful in working out specific relationships.

II. In evaluating the evolutionary processes which are taking place at the present time, we have evidence on three, fragmentation, polyploidy and hybridization.

FRAGMENTATION.

In every species in which we were able to examine a number of different plants, we found individuals with supernumerary fragment chromosomes. That is, in addition to the normal chromosome complement for the species, these individuals had one or two fragment chromosomes, much smaller than the rest (Plate 45, figs. A, K). In at least two cases these fragments paired regularly at the reduction division and were distributed to all the germ cells. We found fragments occurring with roughly the same frequency in all the species which we investigated. If, as seems probable, they affect the external morphology of those plants which bear them, we have here a unique case in which one of the causes of variation within species is not itself effective in forming new species. Had it been so we should have found entire species or races which were characterized by the possession of supernumerary chromosomes.

POLYPLOIDY.

In these species of *Tradescantia* polyploidy is apparently intra-specific, with consequent division of those species possessing it into diploid and tetraploid races. It apparently allows a northern extension of the range in those species in which it has occurred. It increases manyfold the variation between individual plants. Its "blurring" effect upon variation in flower color can actually be demonstrated and a similar effect upon morphological characters is inferred from the peculiar variability of the tetraploid species, *T. reflexa* and *T. virginiana*. In the section of the genus which we have

studied, polyploidy does not occur at the center of specific diversity but is instead characteristic of the northern periphery of the genus. It must therefore be of relatively minor importance as a factor in originating new species though it multiplies the complexity of *inter-specific* and *intra-specific* relationships.

HYBRIDIZATION.

Although this undoubtedly occurs we have as yet found little actual evidence for it. The colony from Hillsboro, described above, may perhaps have resulted from previous hybridization between *T. reflexa* and *T. bracteata*. An apparent example of hybridization between *T. humilis* and *T. reflexa* has just been discovered in the vicinity of Austin, Texas.

SUMMARY

Three species of *Tradescantia* are common in the region about St. Louis, Missouri, two tetraploid species *T. reflexa* and *T. pilosa*, and one diploid species, *T. bracteata*. White-flowered and pink-flowered forms are frequent in *T. bracteata* while in the two tetraploid species they are rare. Furthermore various intermediate magenta shades are common in the tetraploid *T. reflexa* but are not found in *T. bracteata*. This is shown to follow logically from the fact that *T. reflexa* is practically an auto-tetraploid.

Darlington's assumption of highly developed vegetative reproduction in tetraploid *Tradescantias* is found to be without any foundation in fact.

The inter-clonal variation of a single colony is presented in detail.

Seven species of *Tradescantia* from eastern Texas were found to be diploids.

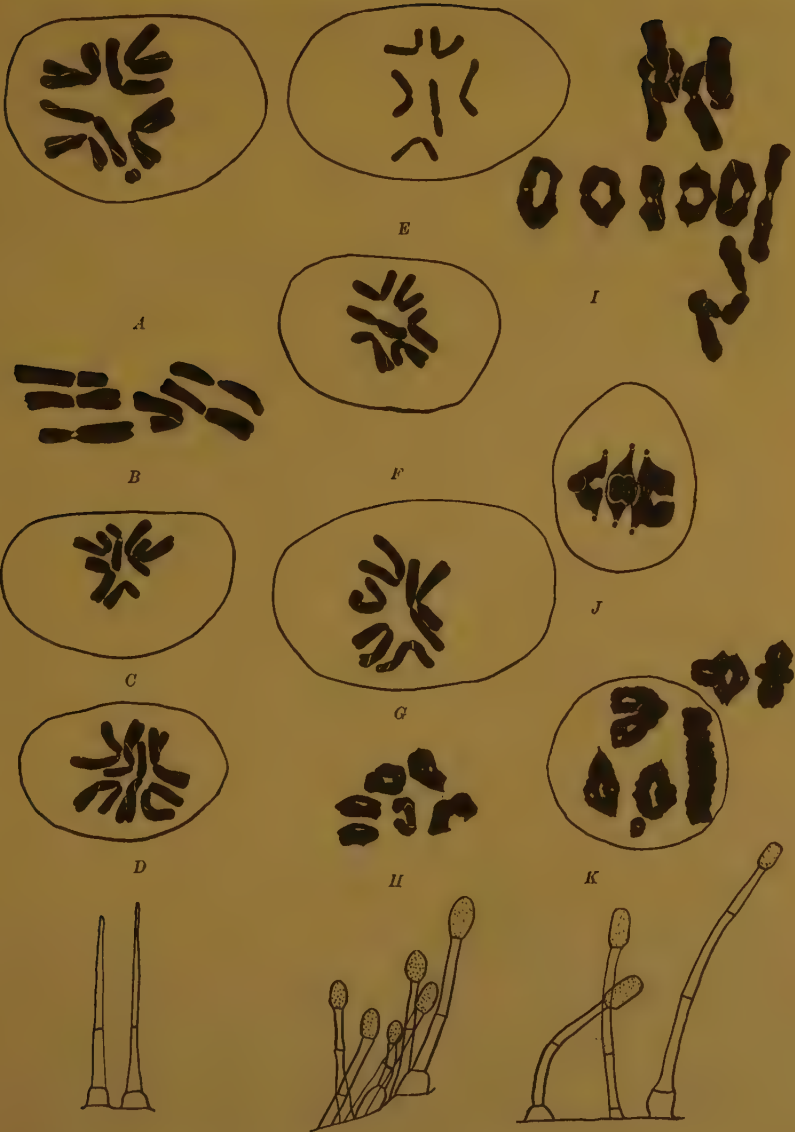
The evolutionary importance of fragmentation, polyploidy, and hybridization is briefly discussed.

ACKNOWLEDGMENT

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CHROMOSOMES AND OVARY HAIRS OF TRADESCANTIA SPECIES

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ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

EXPLANATION OF PLATE 45

Chromosomes of *Tradescantia* species. All drawn with camera lucida at bench level from temporary or permanent smears. I drawn from a plant from eastern Missouri. The others are all from plants collected in the neighborhood of Austin, Texas. In figures I and K the different levels have been drawn separately to avoid confusion.

A. *T. gigantea*. Pollen mitosis. $n = 6 \times f$.

B. *T. texana*. Pollen mitosis. Smear slightly crushed. $n = 6$.

C. *T. humilis*. Pollen mitosis. $n = 6$.

D. *T. edwardsiana*. Pollen mitosis. $n = 6$.

E. *T. occidentalis*. Pollen mitosis. $n = 6$.

F. *T. sp. (reflexa ?)*. Pollen mitosis. $n = 6$.

G. *T. hirsuticaulis*. Pollen mitosis. $n = 6$.

H. *T. humilis*. P M C. 6 bivalents.

I. *T. reflexa*. P M C. 6 bivalents and 3 quadrivalents.

J. *T. humilis*. P M C. Metaphase showing "insertion points."

K. *T. gigantea*. P M C. 6 bivalents and one pair of fragment chromosomes. Two of the bivalents have been drawn at one side for clearness.

Below. Ovary hairs, drawn greatly enlarged with camera lucida. Left, *T. gigantea* from Austin, Texas; center, *T. bracteata* from Portage des Sioux, Missouri; right, *T. pilosa* from Hermann, Missouri.

A COMPARATIVE STUDY OF THREE PHYTOPHTHORA DISEASES OF LILAC AND OF THEIR PATHOGENS

KENNETH S. CHESTER

With a diagram and plates 46 and 47

I. INTRODUCTION

A SERIOUS DISEASE of Lilacs caused by *Phytophthora Syringae* Kleb. has been recognized for many years in European lilac plantings. Very recently a second lilac disease attributed to *Phytophthora cactorum* (L. & C.) Schroet. has been found in America. A third lilac disease due to a distinct form of *Phytophthora* has been under observation at the Arnold Arboretum for several years. The present paper beside first reporting and describing the disease last named and its causal organism also reports a comparative study of the three *Phytophthora* diseases of Lilac with respect to the symptoms, etiology, and control of the diseases in question.

II. HISTORICAL

The first report of a *Phytophthora* disease of Lilac was that of Berkeley in 1881 (4) in which was described under the name *Ovularia Syringae* Berk. a fungus comparable to *Phytophthora infestans* (Mont.) de Bary which caused large brown patches on lilac leaves. Berkeley observed the production of conidia through the stomata and suggested that the conidia might germinate by means of zoospores. The following year Smith (31) first saw the oospores of Berkeley's fungus and described them. The germination of the conidia of Berkeley's fungus by means of zoospores was observed by A. S. Wilson in 1886 (33). Nine years later in 1905 (16) Klebahn published a short account of a disease of Lilac caused by what was in all probability the same fungus as that of Berkeley. The identity of Klebahn's fungus and that of Berkeley was not recognized, however, and Klebahn's disease was attributed to a new species and genus of fungus, *Phloeophthora Syringae* Kleb. According to Klebahn's observations the disease was seated in the cortex of mature lilac branches, was manifested by a browning and death of the cortex, and was apparently not related to any leaf disease. Klebahn succeeded in obtaining pure cultures of the fungus and in producing typical lesions on artificially inoculated plants. Although the sexual structures were seen, there was no apparent production of conidia, which latter fact, together with the location of the disease in the cortex of woody stems, led to the assumption of a new genus.

The following year Klebahn continued his studies (17) and brought out the relation of the disease to the abnormal environmental conditions of the lilac forcing industry. A much more extended account of the same disease is contained in a later work by the same author in 1909 (18), reviewed by Hasselbring in 1910 (13), in which he finally observed the conidia and recognized the true nature of the fungus. The name was accordingly changed to *Phytophthora Syringae* (Kleb.) Kleb. In this longer account Klebahn reported detailed investigations of the symptoms produced on stored and forced Lilacs, the morphology and biology of the fungus, the proof of the parasitism of *Phytophthora Syringae*, and the control measures which had been found to be effective in reducing the disease. In addition to infection experiments with Lilacs, the author also found the fungus to be capable of parasitism of a variety of other host plants. Klebahn's observations showed the disease to be present in 1909 in Hamburg and Cuxhaven, whence he believed it had been introduced from France. Later in 1909 Lustner (24) also reported it from Hohenheim and Frankfurt am Main. In 1910 Himmelbaur (15) repeated Klebahn's studies of *Phytophthora Syringae* and confirmed the latter in finding *P. Syringae* distinct from any previously reported species of *Phytophthora*.

By 1913 the fungus had spread to Holland according to the report of Schoevers (29) and was there likewise found to be causing a serious disease of cultivated lilac plants. The following year G. W. Wilson studied *P. Syringae* from the taxonomic standpoint (34), and beside confirming the earlier descriptions of the fungus the author was the first to point out the probable identity of Klebahn's fungus with that of Berkeley's. The name *Phytophthora Syringae* (Kleb.) Kleb., however, is retained. In 1918 Arnaud (1, 2) reported the appearance of the disease in France, where it was causing minor injury in a hedge of Lilac. Here for the first time the conidiophores of *Phytophthora Syringae* were observed occurring in nature on infected Lilacs.

Up to 1922 the disease had been reported from England, Germany, France, and Holland. In that year Lafferty and Pethybridge (19) reported an isolation of *Phytophthora Syringae* from rotted apple fruit in Ireland. Specimens of lilac leaves probably injured by *P. Syringae* had also been received by the same authors. In the paper in question the authors reviewed the morphology of the sexual organs of *P. Syringae* and reported for the first time the presence of both amphigynous and paragynous antheridia within the species.

Phytophthora Syringae was shown to be capable of saprophytic life in the soil by de Bruyn in 1922 (5). Two years later Miss de

Bruyn published a continuation of her studies (6, 7) in which were reported an extensive series of infection experiments on Lilac. In the latter papers she found that the disease occurred in greatest destructiveness in those seasons in which there was abnormal rainfall in August or September. Infection was found to take place in the winter months, from December till April in the cortex, and from October till February in the buds. Hand picking of the leaves as a control measure was suggested, but in a later paper (8) the author found that hand picking of the leaves was so injurious to the blossoms as to eliminate it as a control measure.

The only record of *Phytophthora Syringae* in America is that of Hedges in 1929 (14). Miss Hedges found a fungus believed to be *P. Syringae* fruiting on several blighted young lilac shoots in Washington. The lesions had the appearance of those due to fire blight (*Bacterium Syringae*), and the attack was severe. Since the lesions described were on young shoots examined in May, it is possible that the *Phytophthora* found was one of the other two species here considered, since *P. Syringae* normally does not primarily attach the succulent tissues of lilac.

Phytophthora cactorum (L. & C.) Schroet., originally described as *Peronospora cactorum* by Lebert and Cohn in 1870 (20) and since investigated by many workers, is known to parasitize a great variety of host plants. On Lilac, however, it has been recognized only recently. In 1929 R. P. White described a disease of *Rhododendron* and Lilac from New Jersey, with which was associated this species of *Phytophthora* (35). Cross infection experiments proved that the same fungus was responsible for the disease in both hosts. On Lilac the disease takes the form of a dying-back of suckers and of leaf infections. Production of conidia was observed on the Lilac. As control measures for Lilacs, White suggested generous spacing of the plants, removal of dead wood, and use of a dormant spray of lime-sulphur together with summer applications of Bordeaux mixture.

With regard to the third type of *Phytophthora* causing disease in Lilac, no record has heretofore appeared in the literature.

In addition to the primarily pathological literature dealing with the lilac *Phytophthoras*, a number of purely mycological papers have dealt with *P. Syringae* and *P. cactorum*. An attempt will not be made to go into the taxonomy of these species at the present, but it may merely be said in passing that the two species are considered perfectly distinct by all of the leading students of the genus (G. W. Wilson, 1914, 34; Rosenbaum, 1917, 26; Leonian, 1925, 21; Tucker, 1931, 32).

III. MATERIALS AND METHODS

The cultures of *Phytophthora* employed in the present study were obtained from the following sources: (a) a culture of *Phytophthora Syringae* isolated by Miss de Bruyn from Lilac in Holland and obtained from the Centraalbureau voor Schimmelcultures at Baarn in 1928; (b) a culture of *Phytophthora cactorum* isolated from Lilac in New Jersey by R. P. White and sent to me by Dr. White in 1929; (c) several cultures of the same organism isolated from Lilac by the writer in 1929; (d) a third distinct strain isolated from Lilac in the Arnold Arboretum by the writer in 1929 and hereafter referred to as *Phytophthora* "Type A."

Stock cultures of the various strains were maintained on potato-dextrose agar. For the production of the spore forms special techniques were necessary. None of the strains produced sporangia in appreciable amount on potato-dextrose agar. For sporangium production the technique originally devised by Klebs was employed. Tiny fragments of mycelium of active cultures were transferred to large test-tubes each containing about 20 cc. of pea decoction. After several days growth in the pea broth at room temperature the mycelial mats were transferred to sterile pond water, the sterile water being renewed frequently. Distilled water did not prove satisfactory for this purpose. Abundant production of sporangia resulted at room temperature within 24 to 48 hours after transferral to sterile water. The production of sporangia was also induced by the conventional employment of Petri's mineral solution

(.4 gm. $\text{Ca}(\text{NO}_3)_2$ + .15 gm. KH_2PO_4 + .15 gm. MgSO_4
+ .06 gm. KCl + 1000 cc. H_2O),
although Petri's technique proved much less satisfactory than that of Klebs for the species of *Phytophthora* involved.

Oospore formation was brought about by the employment of special solid media, the requirements differing for the different strains of *Phytophthora* under consideration. *Phytophthora cactorum* readily reproduced sexually on a wide variety of solid substrata. Among these steamed corn-meal, steamed green bean pods, steamed carrot, lima bean agar, oatmeal agar, and corn-meal agar proved very favorable. *Phytophthora Syringae* produced oospores with apparent difficulty, sterile lilac leaf extract (10), steamed carrot, steamed corn-meal, and oatmeal agar in the order named yielding the most satisfactory results. *Phytophthora* "Type A" produced oospores abundantly on steamed green bean pods, lima bean agar, and corn-meal agar.

Since the morphology and the physiology of the genus *Phytoph-*

thora are subject to considerable variability according to the type of substrate employed, the reactions of the lilac *Phytophthoras* to various artificial media were studied in detail. The following media were used to this end:

Steamed corn-meal	} Prepared according to the formulas of Tucker (32).
Steamed green bean pods	
Potato-dextrose agar	
Lima bean agar	
Oatmeal agar	
Potato-dextrose agar	(Filtrate of 200 gm. boiled potato + 25 gm. agar + 30 gm. bacto-dextrose + water to make 1000 cc.).
Malt agar	(50 gm. malt extract + 25 gm. agar + water to make 1000 cc.).
Prune agar	(50 gm. dried prunes + 25 gm. agar + water to make 1000 cc.).
Pea broth	(Filtrate from 50 gm. dried split peas boiled until soft + water to make 1000 cc.

Steamed carrot cylinders.

In addition to the media indicated above, corn-meal agar with the addition of certain stains was employed in a brief study of the penetration of dyes *in vivo*.

The observations of the *Phytophthora* diseases in nature and the study of the physiology, morphology, and taxonomy of the fungi involved were supplemented by an investigation of the pathology of the various strains of *Phytophthora*. For this purpose several series of inoculation experiments were performed in which the strains of *Phytophthora* under consideration were inoculated into a variety of Oleaceous plants. Such inoculations were of various form, consisting of insertions of mycelium into injured leaf and stem tissues, placing of mycelium upon unbroken plant parts, and finally permitting suspensions of freshly liberated zoospores to come into contact with the plant tissues. The inoculated plants were retained in an Arnold Arboretum research greenhouse under conditions favorable for their growth, and the inoculations were protected in the conventional manner.

Finally, all of the available literature pertaining to the *Phytophthora* diseases of the Lilac was carefully assembled and compiled. The bibliography at the end of this paper accordingly contains a virtually complete list of the references to scientific studies dealing with one or another phase of the problem of *Phytophthora* disease in Lilacs.

IV. COMPARATIVE STUDY OF THE SPECIES OF
PHYTOPHTHORA PARASITIZING LILAC

As a preliminary to a correct diagnosis of the *Phytophthora* diseases of Lilac and to a correct determination of the rôle played by the fungi involved in causing disease, a study of the comparative mycology of the fungi was essential. Such a study has been in progress and the experimental results and interpretations will be the subject for consideration in the present section. For convenience the experimental findings are grouped under the headings of physiology, morphology, and systematics.

A. PHYSIOLOGY

The genus *Phytophthora* has long offered to systematists a difficult problem. The morphological characters by which species of fungi are separated must necessarily be relatively invariable within the species in order that the specific differences may be determined with accuracy. Where clear cut morphological differences are lacking, as in the bacterial genera, the systematist is forced to turn to the more striking physiological characters as bases for specific distinction. The taxonomic studies of *Phytophthora*, first based upon what were believed to be sharp morphological criteria, have undergone a gradual evolution from purely morphological systems to those almost purely physiological. The reason for such an evolution in approach has been that many of the morphological characters formerly assumed to be constant within a species have since proved to be capable of wide variation according to the physiological environment. Thus the position of the antheridium relative to the oogonium was at one time felt to be a constant character in *Phytophthora* species. The work of Lafferty and Pethybridge (19) however has shown that in many species of *Phytophthora* both amphigynous and paragynous antheridia occur, although there is a tendency in a given species to form the great majority of the antheridia in one or the other manner. The size of the reproductive organs, again a character which is usually dependable in the fungi, is susceptible to such wide variation in *Phytophthora* that the only findings yielding results at all satisfactory are those based on extensive biometric studies. Other characters of the species such as method of conidial germination, method of zoospore germination, mycelial characters, and sexuality likewise exhibit high degrees of variability within a given species. Accordingly any mycological study such as the present one must necessarily be concerned both with physiological and morphological characters. Among the physiological criteria which may effectively be applied to *Phytophthora* are the rate and

type of growth upon various artificial media, the production of fructifications upon various media, and the relationship of temperature and pH to rate of growth. Accordingly these various physiological factors in relation to the lilac *Phytophthoras* will be discussed at this point.

RATE AND TYPE OF GROWTH ON VARIOUS MEDIA. During the three years in which the lilac *Phytophthoras* have been a subject of study in this laboratory they have been grown on a wide variety of nutrient substrata. Freshly-made media were always employed, made according to the formulae given in the preceding section. For the preparations of fresh vegetable products small wide-mouthed vaseline bottles were used as receptacles, while for the other media both culture tubes and Petri dish cultures were employed. All of the cultures indicated below were grown at a room temperature of 21° C. The results of these experiments are indicated in the table on pages 239-240. The terms used in description of the mycelium are those of Long and Harsch (23).

It is at once apparent from a consideration of the foregoing data that there is a distinct difference in behavior toward the various media of the three strains of *Phytophthora* at hand. On the whole *Phytophthora Syringae* is more divergent from the remaining two species than the latter are from each other. This greater divergence of *P. Syringae* is particularly evident in its weaker growth on all media. On the whole *Type A* resembles *P. cactorum* in the general features of its growth reactions. On the other hand, a number of differential reactions set it apart from *P. cactorum*. Thus one finds aërial mycelium in *Type A* on oatmeal, corn-meal, malt, and prune agars, while the mycelium of the other strains is wholly appressed on these media. The aërial mycelium of *Type A* is characteristically different from that of *P. cactorum*, being longer, relatively less branched, and frequently with a silky sheen. The three strains are perhaps most strikingly differentiated on steamed carrot slants. *P. Syringae* grows much more slowly than the other strains on this substrate at room temperature, its growth being very slight during the first week while the other two strains are able to occupy the entire slant in that time. Moreover *P. Syringae* is white with much aërial mycelium at the edges of the colonies. *P. cactorum* and *Type A* are both much more sodden. *Type A* is white except as the sodden appearance makes it difficult to determine the color, while *P. cactorum* is noticeably discolored due to myriads of oospores, its color being clay-color (Ridgeway). The powdery-sodden appearance of *P. cactorum* is also readily distinguished from the silky-sodden appearance of *Type A*. Thus a consideration of the manner and extent

TABLE 1. RATE AND TYPE OF VEGETATIVE GROWTH OF THE LILAC PHYTOPHTHORAS ON VARIOUS MEDIA (21° C.)

SUBSTRATE	DAYS AFTER INOCULATION	PHYTOPHTHORA SYRINGAE	PHYTOPHTHORA CACTORUM	PHYTOPHTHORA "TYPE A"
Steamed corn-meal.	6	Mycelium extensive but thin, not forming a cottony mass. Colony more than 5 cm. in diameter.	As in <i>P. Syringae</i> .	As in <i>P. Syringae</i> .
	14	Mycelium as at 6 days.	As in <i>P. Syringae</i> .	As in <i>P. Syringae</i> .
Steamed green bean pods	11	Mycelium sodden and felty, not as extensive as in the following two strains. Colony about 3 cm. diameter.	Mycelium cottony to felty, forming a distinct pellicle over water. Colony about 5 cm. diameter.	Mycelium cottony, rather thinner than the last, forming a pellicle over water. Colony about 5 cm. diameter.
	14	Mycelium as at 6 days.	Mycelium as at 6 days.	Mycelium now more cottony than in the other strains.
Lima-bean agar	6	Mycelium appressed, none aërial whatever. Colonies only 2.5-4.0 cm. diameter.	Mycelium cottony to felty, compact, denser and shorter than in the next. Colonies 5.0-6.5 cm. in diameter.	Mycelium almost cobwebby, thin but long except at the margin of the colony where there is a 5 mm. zone which abruptly becomes appressed. Colonies 5-6 cm. diameter.
	14	As at 6 days.	As at 6 days.	As at 6 days. Hyphae long, thin, relatively unbranched.
Oatmeal agar.	6	Mycelium completely appressed. Very thin and difficult to see. Colonies 2-4 cm. diameter.	Mycelium completely appressed but much more easily distinguished than the last because not so thin. Colonies 7-9 cm. diameter.	Considerable aërial mycelium present, cobwebby-downy but thin and distinguished with some difficulty. Colonies 7-9 cm. diameter.
	14	As at 6 days.	As at 6 days.	Much aërial mycelium present though none on the other two strains.

TABLE 1—Continued

SUBSTRATE	DAYS AFTER INOCULATION	PHYTOPHTHORA STRINGAE		PHYTOPHTHORA CACTORUM		PHYTOPHTHORA "TYPE A"	
		5		6		7-9	
Corn-meal agar.....		Mycelium completely appressed, very thin and distinguished with difficulty. Colonies 2.5-3.5 cm. diameter.		Mycelium completely appressed, thin but extensive. Colonies 7-9 cm. diameter.		Mycelium much as in the last, thin, appressed, but becoming aerial (cobwebby) at the lower end of the slant. Aërial mycelium distinguished with difficulty. Colonies 7-9 cm. diameter.	
Potato-dextrose agar....	11	Mycelium as at 6 days. No aërial mycelium.		Mycelium as at 6 days. No aërial mycelium.		Aërial mycelium plainly visible.	
	6	Mycelium sodden and slightly downy. Colonies 3 cm. diameter.		Mycelium subfely, not at all sodden, rather compact, not long and silky as in the next. Colonies 5-6 cm. diameter.		Mycelium cottony with a silky sheen. Hyphae long. Colonies 6-8 cm. diameter.	
	14	Growth moderate, sodden or slightly downy. Zonate in daylight.		Growth moderate, subfely, azonate in daylight.		Growth strong, cottony, azonate in daylight.	
Malt agar.....	5	Almost no growth.		Moderate, more or less sodden growth.		Extensive downy growth.	
	14	Growth weak, appressed.		Growth moderate, appressed to downy.		Growth strong, appressed.	
Prune agar.....	2	No growth.		Growth moderate, thin, appressed.		Growth strong, appressed to cobwebby.	
	14	Growth very weak, appressed.		Growth moderate, appressed.		Growth strong, downy.	
Steamed carrot.....	10	Growth very weak, downy.		Growth moderate, fely.		Growth strong, woolly.	
	20	Growth weak. Downy, becoming sodden at the center.		Sodden but with such a covering of oospores as to give it a powdered appearance. Aërial mycelium downy where it appears (at center of colony only).		Sodden with none of the powdery appearance of the last. The scanty aërial mycelium is very silky.	
Pea broth.....	3	Growth weak. Colonies .5 cm. diameter.		Growth strong. Colonies about 2.5 cm. diameter.		Growth strong. Colonies about 2.5 cm. diameter.	

of growth upon various media offers evidence as to the existence of three distinct strains of *Phytophthora* parasitizing Lilac.

PRODUCTION OF FRUCTIFICATIONS ON VARIOUS MEDIA. A second type of physiological evidence is yielded by a study of the ability of *Phytophthora* to produce asexual and sexual reproductive organs on various media. Such a study has been carried on with reference to the lilac *Phytophthoras* and the results are summarized in Table 2 on page 242. The cultures were all made in the conventional manner, the normal pH of the cultures was not altered, and the cultures were all grown at 21° C except as otherwise indicated. In the section entitled "Klebs' technique" the fungi were grown for four or five days in sterile pea broth and then transferred to sterile pond water, the water being changed twice daily.

The data in Table 2 again reveal the striking difference between *P. Syringae* and the other two strains, although the latter two behave in a rather similar fashion with regard to the production of fructifications. Oogonia are apparently formed with some difficulty in *P. Syringae* and are absent on a number of media on which the other two fungi produce them in abundance. At the other extreme is *P. cactorum* which produces oogonia on many media in surprising numbers. For example it was seen in temperature experiments that *P. cactorum* will cover a Petri dish of corn-meal agar with a profusion of oospores in 4 days at 25° C. *Type A* behaves in an intermediate manner, forming numerous oospores on a variety of media but never to quite the same extent as *P. cactorum*. Except by the employment of Klebs' principle of suddenly removing the food supply, the production of sporangia is very limited in all the strains. None have ever been observed in artificial cultures of *P. Syringae* except as grown by the Klebs and Petri techniques. Frequently the sporangia formed in artificial culture are very irregular or abortive in form, being non-functional in the form of moniliform swellings on the hyphae, functional but bi-papillate, greatly elongated or asymmetric, etc. From the data presented one may conclude that with respect to the character of fructification on various media, *P. Syringae* is perfectly distinct from the other strains, while the latter, although resembling each other in the main do differ significantly in a number of features.

RATE OF GROWTH AT DIFFERENT TEMPERATURES ON THE SAME MEDIUM. A third physiological factor of value in differentiating species and of great importance in the economic considerations of *Phytophthora* diseases is temperature. Differential growth according to temperature has been seen to be of such value in species diagnosis that it ranks among the most useful characters on which

TABLE 2. PRODUCTION OF REPRODUCTIVE ORGANS BY THE LILAC PHYTOPHTHORAS ON VARIOUS MEDIA

MEDIUM	DAYS AFTER TRANSFER	P. SYRINGAE		P. CACTORUM		PHYTOPHTHORA TYPE A	
		SPORANGIA	OOGONIA	SPORANGIA	OOGONIA	SPORANGIA	OOGONIA
Steamed corn-meal.....	14	None	Frequent	None	Very abundant	None	Present, not abundant
Steamed bean-pods.....	14	None	None	Infrequent	Very abundant	None	Abundant
Potato-dextrose agar.....	14	None	None	Frequent	Fairly abundant	Very infrequent	Present, not abundant
Lima-bean agar.....	14	None	None	Numerous	Abundant	None	Abundant
Oatmeal agar.....	14	None	Present, not numerous	None	Numerous	None	Abundant
Corn-meal agar.....	14	None	Very infrequent	Not infrequent	Numerous	None	Numerous
Klebs' technique (21° C.)	1	None	None	None	Abundant	None	None
	2	Present	None	Numerous	Abundant	Numerous	None
	3	Present	None	Numerous	Abundant	Numerous	None
	4	Numerous	None	Numerous	Abundant	Numerous	None
Klebs' technique (8° C.)	1			None	None	None	None
	2			None	None	None	None
	3			Present	None	None	None
	4			Present	None	Present	None
Petri's mineral solution.							
From culture on:							
A. Corn-meal agar.....	5	Present, not abundant		Present, not abundant		Absent	
B. Potato-dex. agar.....	5	Absent		Infrequent		Infrequent	
C. Lima-bean agar.....	5	Very infrequent		Very infrequent		Infrequent	

recent *Phytophthora* keys are based, Hence it was thought desirable briefly to investigate the behavior of the *Phytophthora* strains under consideration at different temperatures. It proved practicable to work only with the temperatures above 21° C, but since *P. Syringae* is apparently the only strain of the three at hand which vegetates extensively at the cooler temperatures and since the temperature relations of *P. Syringae* have been studied in detail by previous workers, the data at hand are sufficient to indicate the pronounced differences between the three strains. The temperature study reported here was conducted with the fungi growing on homogeneous lots of corn-meal agar in constant temperature chambers with a temperature variation of no more than .5° C. Thirty plates of each fungus were used at each temperature. The results may be briefly summarized as follows.

At 29° C. none of the lilac strains of *Phytophthora* made appreciable growth. At 27° C. *P. Syringae* failed to grow as did most of the cultures of *Type A* and *P. cactorum*, although a few scattered cultures of each of the latter two strains showed a very limited growth. At 25° C. *P. Syringae* failed to grow, but *Type A* and *P. cactorum* grew very extensively, the colonies being from 75 to 90 mm. in diameter after 96 hours. Numerous oospores were present in the cultures of these latter strains after 96 hours. This temperature appears to be very near the optimum for both *Type A* and *P. cactorum*, as the growth is far more extensive at 25° C. than at room temperature. The upper limit of growth for *P. Syringae* is approximately 23° C., and the optimum, according to my own observations and to Tucker's more critical studies (32), is about 20° C. Thus a clear-cut distinction according to temperature requirements exists between *P. Syringae* and the other lilac strains of *Phytophthora*. *P. Syringae* grows best at 20° C., a temperature at which the growth of *Type A* and *P. cactorum* is only indifferent, while at 25° C., the optimum temperature for both *Type A* and *P. cactorum*, the growth of *P. Syringae* is wholly inhibited. Apparently the lilac strain of *P. cactorum* is somewhat less resistant to heat than the strains of *P. cactorum* studied by Tucker, all of which vegetated at least to 27.5° C. and some to 30° C. The practical bearing of temperature requirements of the lilac *Phytophthoras* will be considered later in relation to their pathology.

RELATION OF GROWTH TO HYDROGEN ION CONCENTRATION. A fourth physiological characteristic useful in distinguishing *Phytophthora* species is the relation to hydrogen ion concentration. In order to investigate this matter an experiment was devised in which the fungi were permitted to vegetate in liquid media of varying hydro-

gen ion concentrations. Pea broth was selected as the medium to be used, since all three strains of *Phytophthora* from Lilac grow well in this decoction. A single large flask of pea broth was filtered and then divided into 16 equal portions. One portion was retained without altering the normal pH, which was found to be 6.5. The other portions were titrated with decinormal HCl and KOH to a series of pH values extending from 2.5 to 10.0 at .5 pH intervals. The pH determinations were made colorimetrically by the use of Clark's indicators. Each portion was now divided into three equal samples of 15–20 cc. each, the samples being placed in 6 x 1" test tubes. The 45 tubes were then autoclaved and finally all the tubes of each complete series of pH values were inoculated with *P. Syringae*, *P. cactorum*, and *P. Type A* respectively. The fungi were permitted to develop for 5 days at room temperature at the end of which time the amounts of growth were compared. The results are given in the following table:

	PH OF MEDIUM:															
	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0
<i>P. Syringae</i>	0	0	3	4	4	4	4	4	4	3	1	0	0	0	0	0
<i>P. cactorum</i>	0	2	3	4	4	4	4	4	4	4	4	4	4	2	2	2
<i>P. Type A</i>	0	2	3	4	4	4	4	4	4	3	3	3	3	2	2	0

(KEY: 0—No growth; 1—Very weak growth; 2—Weak growth; 3—Moderate growth; 4—Strong growth.)

The results of this experiment confirm the earlier findings in demonstrating *P. Syringae* to be markedly distinct from the other two lilac strains of *Phytophthora*. The latter two show virtually no difference, however, in their pH reactions. The extremely long pH range of all three of these strains, particularly the latter two, is worthy of note, and the high degree of toleration exhibited argues against the possibility that the pH reaction of host tissue might play a part in the immunity or susceptibility of a given host subject to these strains of *Phytophthora*.

In relation to the preceding experiment in hydrogen ion control, an experiment was also performed in which was investigated the ability of certain dyes to penetrate the living *Phytophthora* cell. The experiment took the following form. A litre of clear corn-meal agar was prepared in the customary fashion. When liquid this was divided into a number of portions, to which portions were added the following stains in concentration of 6–10 drops of 1% stain solution per 50 cc. of agar: acid fuchsin, phenol red, methyl red, cresol red, and neutral red. A portion without stain was retained as a control. Samples of each portion were then poured into a number of sterile Petri dishes and inoculated with the three lilac strains of *Phytoph-*

thora. As certain of the stains used are pH indicators (phenol red, cresol red), the variations in pH during growth could be read directly. The original pH of the agar was 6.4. After 14 days *P. cactorum* and *Type A* had raised this to 7.4 in the areas occupied by mycelium, although *P. Syringae* had not changed the original pH of the agar. Methyl red appeared to have a repressing or toxic effect on *P. cactorum* and on *Type A*, but not on *P. Syringae*. On the other hand, neutral red exerted such an effect upon *P. Syringae* but not on the other two strains. None of the other stains appeared to affect the development of the mycelium or oospores.

All of the dyes used stained the oospore walls of *P. cactorum* and *Type A* brilliantly. (No oospores were formed in *P. Syringae*.) These were the only structures stained *in vivo* with phenol red, cresol red, methyl red, or acid fuchsin. In order to be certain of the presence or absence of vital staining, the mycelium was permitted to grow out on sterile cover-glasses which were later removed and examined for the presence of dye within the hyphae. Since *Phytophthora* is coenocytic, a dye which could penetrate should be carried out into such isolated hyphal stretches and thus be easily identified. The streaming of the protoplasm meanwhile offered a check as to the living condition of the hyphae. Neutral red penetrated the cytoplasm of the fungi and accumulated in the vacuoles, and could be identified far out on the sterile cover-glasses. This staining *in vivo* was accentuated when the mycelium was placed in a mildly alkaline buffer solution as an adjunct to staining. The staining of the vacuoles by neutral red but not by methyl red demonstrates that the vacuoles in these fungi are of the type designated by Bailey as "Type B" (3).

A marked reduction of the dye occurred in all the cultures containing methyl red, although such a dye reduction was not observed in the cases of the other dyes.

The evidence from this latter experiment accordingly confirms that obtained in the preceding experiments in demonstrating the similarity of reaction of *P. cactorum* and *Type A* in contrast to the marked divergence of *P. Syringae*.

B. MORPHOLOGY

Passing from a physiological to a morphological comparison of the three *Phytophthora* strains from Lilac, one finds that although there are certain resemblances there are also clear-cut and constant differences which readily distinguish the three strains from one another. The morphological comparison can best be pursued by considering successively the vegetative body, the asexual reproduc-

tive structures, the sexual reproductive apparatus, and finally the abortive reproductive structures so commonly found in this group of fungi.

VEGETATIVE BODY. The mycelium of all three strains of *Phytophthora* from Lilac is typical for the genus. In all cases the hyphae are highly granular and vacuolate, irregular in diameter and branching, and for the most part non-septate except at the bases of the reproductive structures and in old hyphae. Streaming of the protoplasm is customarily observed in all the strains, particularly in actively growing cultures in the main hyphae supplying the peripheral branch systems. This streaming is rapid and in all cases takes the form of an oscillation rather than a cyclosis as in the higher plants, the period of oscillation being from one to several minutes.

In order to obtain an accurate basis for comparison of the mycelial characters of the three strains, cultures were made on cornmeal agar and examined critically after one week's growth at room temperature. The following descriptions were made from examinations of such cultures.

In *Phytophthora Syringae* the branching is monopodial with the lateral branches irregularly distributed along the main axes and typically at right angles to the latter. The laterals are frequently constricted at the point of junction with the main axes and are poorly developed with relation to the main axes. Septations are very infrequent, are curved with the direction of curvature bearing no relation to the direction of growth, and are perforate. The diameter of the hyphae is variable, usually, however, fluctuating between 3 and 7 microns. The hyphae are granular or with extended vacuoles. Streaming is frequent and rapid.

In *P. cactorum* the branching is irregularly monopodial although sometimes approaching dichotomy. The lateral branches are more highly developed than in *P. Syringae*, are typically at right angles to the main axes, and are frequently much constricted at the junctions with the main axes. The hyphae are very granular and with fewer vacuoles than in *P. Syringae*. Septations are very infrequent, being found for the most part in empty hyphae, and are curved. The diameter of the hyphae is much more variable than in *P. Syringae* although the customary limits are between 3 and 7 microns. Streaming is frequent and rapid.

In *Type A* the hyphae are much more highly branched than in either of the preceding species on this substrate. The branching is typically monopodial but often becomes nearly dichotomous. The laterals may be perpendicular to the main axes, but more frequently they leave at an angle of between 50° and 70°. The hyphae, which

are finely granular, are more delicate and more even in diameter than in *P. cactorum*, varying between 2 and 6 microns in diameter. Septations are very infrequent and as in the species preceding are curved. The lateral branches are frequently constricted at their junctions with the main axes. Streaming is frequent and rapid.

The descriptions above apply exclusively to the aërial and superficial mycelium, the submerged mycelium being frequently very abortive in appearance. In all three strains there is a tendency for the mycelium of old cultures to assume an atypical condition, and this is particularly true of *P. Syringae*, where the hyphae of old cultures are often knotty, vesicular, and highly irregular.

In connection with the experiments in vital staining reported above, an interesting reaction to food supply was observed in *Type A* and later confirmed in the other species. Sterile cover glasses had been dropped onto the surface of the agar in newly made corn-meal agar cultures. The growing mycelium coming into contact with the sterile glass surface in many cases grew out onto the latter for a distance of one or more millimeters. As each hypha grew out onto the glass it produced a fairly complex system of lateral branches. Eventually, however, the dendritic system reached such proportions that the main hypha could no longer maintain a sufficient supply of nutrients for its needs. The reaction of the branch system was as follows. First a complete septation occurred near the edge of the cover slip in the main hypha. The protoplasm of the main hypha then retreated for a distance of about 10 microns and a second septation then separated the empty hyphal stretch from the retreating protoplasm. If any side branches lay along the unoccupied stretch of hypha, these also emptied into the retreating mass. Soon the process was repeated. A second retreat followed by a second septation was observed. This process continued until there were 10 or more septations in the empty section of hypha. Meanwhile the protoplasm of the more peripheral branches of the dendritic system was likewise receding, always marking the path of retreat by successive septations. In brief the protoplasm of the whole dendritic system was becoming condensed in the center of the dendritic mass, and the protoplasm was maintaining its life at the expense of a portion of itself. The remaining protoplasm was alive and active, and presumably would continue so until it had entirely consumed itself.

ASEXUAL REPRODUCTIVE STRUCTURES. The morphology of the asexual reproductive organs, in particular the zoosporangia, is of prime importance in the distinction of the strains of *Phytophthora* from Lilac, because herein lies the most important difference between *Type A* and *P. cactorum*, the two strains which up to the present have been seen to differ only in minor characteristics.

In general structure the sporangia of all three of the strains are wholly typical for the genus. They arise terminally on relatively undifferentiated sporangiophores, singly or in sympodial clusters, the successive sporangiophores always arising below the base of the preceding sporangium, never passing through the empty sporangium preceding as in the group of *P. cryptogaea*. No essential differences in development of the sporangia of the three lilac strains of *Phytophthora* have been observed. However, the character of the papilla of emergence of the zoospores is markedly different in the lilac *Phytophthoras*. The papilla of *P. cactorum* is of the more common form in the genus, prominent, sometimes even approaching cylindrical in shape. The papillae of the other two strains, on the contrary, are flattened, inconspicuous, crescentic in vertical section. That the type of papilla is a relatively fixed character is seen in the prominence given to this character in the recent taxonomic studies of the group. The papillae of *Type A* are so wholly distinct from those of *P. cactorum* that there is no danger of confusing the two even with a cursory examination of the sporangia, and in the many conditions of sporangium production observed, the character of papilla remained constant. That there is also a difference in the chemical composition of the papillae in *Type A* and *P. cactorum* is evident from the fact that the papillae of *P. cactorum* are often either dissolved or rendered invisible in Amann's lacto-phenol preparations, while those of *Type A* remain perfectly distinct under the same conditions. The types of papillae in the three lilac strains of *Phytophthora* are illustrated in Figures 1-24 of plate 46.

The lilac strain of *P. cactorum* is also distinguished from the other two strains by the fact that the sporangia are much more likely to be deciduous. If water cultures containing quantities of the sporangia of the three lilac strains of *Phytophthora* be shaken vigorously, many of the sporangia of *P. cactorum* will become detached, while those of the other two strains do not become detached to appreciable extent. The detached sporangia of *P. cactorum* each bear a tiny stump of the conidiophore, but these stumps are so short (being no more than half as large as the papillae of the same sporangia) that they could hardly be considered pedicels. In any case there is no evidence of the presence of pedicels in *P. Syringae* or in *Type A*, a point which will be considered in the systematic discussion to follow.

The mature sporangia typically emit zoospores in the customary fashion in the three lilac strains, and no significant differences in the three strains in mode of emission or in number, structure, or behavior of the zoospores were observed.

The released zoospores swim vigorously for a period of the order of an hour or less. They then come to rest, round off, lost their flagella, and germinate shortly. The rapidity of germination and the length of the germ tubes produced are astonishing. For example in one experiment in which freshly liberated zoospores were permitted to germinate in sterile pond water, the total length of hypha resulting from typical spores after 24 hours was measured. Such measurements gave for *P. Syringae* 270 microns, 315 microns, 210 microns, 227 microns, 217 microns, etc., for *P. cactorum* 210 microns, 112 microns, 158 microns, 227 microns, 158 microns, etc., and for *Type A* 402 microns, 356 microns, 140 microns, 368 microns, 315 microns, etc. One frequently observes that in the germination of the zoospores the limited amount of protoplasm passes to the tip of the growing germ tube, so that a germinated spore would typically show an empty spore case produced out into a long germ tube, the proximal portion of which would be empty, and the distal growing portion rich in protoplasm.

Studies were made of the measurements of the sporangia, but since no significant difference was found in the three strains under consideration and since the measurements of the sporangia of any one strain vary within extremely wide limits, no attempt will be made to differentiate the three according to this character. In the majority of sporangia of all three types the length varies from 20 to 40 microns and the width from 15 to 30 microns. There is also no significant difference in the ratio of width to length, this constant averaging in all the strains between .65 and .80.

SEXUAL REPRODUCTIVE STRUCTURES. The most fundamental morphological character in the separation of species of *Phytophthora* has been the type of antheridium, whether amphigynous (surrounding the oogonial stalk) or paragynous (not surrounding the oogonial stalk). Although Lafferty and Pethybridge (19) and others subsequently have shown that both amphigynous and paragynous antheridia may occur within the same species, yet all described species in which the sexual structures occur are characterized by having a distinct majority of the antheridia of one type or the other. The amphigynous type is by far the commoner in the genus, and it is very interesting to observe that the antheridia are chiefly paragynous in all of the lilac strains, although according to Tucker's conception (32) no other valid species than *P. cactorum* and *P. Syringae* possess a majority of paragynous antheridia. The antheridia of *Type A* are perfectly typical for the paragynous type and differ in no essential from those of *P. cactorum* and *P. Syringae*, as will be seen from an examination of Figures 27-30 of Plate 47. In all the

species here involved they are long persistent and are chiefly basal, only occasionally being lateral in position.

In all three strains the oogonia are broadly clavate to subspherical or spherical and usually terminal. The oospores are in all cases spherical, hyalin to light yellow, with the contents granular and variously vacuolate, and with a thick triple wall. The character of this wall appears to differ somewhat in *Type A* from the other two strains. In the latter it is smooth, while in *Type A* under some conditions it appears to be surrounded by a granular aura. The size of the oospores was investigated by employing statistical methods, as the variability is so great within a species as to require such a procedure. Measurements were made of 400 living oospores of each of the three strains, the measurements were grouped into classes, the frequencies plotted, and the constants calculated. The results are given in Text figure 1.

The following constants were derived from the data obtained:

	P. CACTORUM	TYPE A	P. SYRINGAE
Mean (in microns).....	22.94 ± .06	24.97 ± .09	31.10 ± .11
Median (in microns).....	22.79	24.92	31.68
Mode (in microns).....	21.36	24.92	32.04

It will be seen that the measurements for *P. Syringae* are slightly greater than those found by other investigators (the mean usually being in the neighborhood of 28 microns). However, the difference between the measurements of *P. Syringae* and those of the other two strains is sufficiently great that it is considered significant in the distinction of the species. On the other hand, the difference in measurement between *Type A* and *P. cactorum* is so slight, in comparison with the variations within *P. cactorum*, that that difference is not felt to be significant for the purposes of species distinction.

Phytophthora omnivora is known to be heterothallic (22). Other species, such as *P. Cinnamomi*, *P. cryptogaea*, *P. Richardiae*, and *P. Phaseoli*, appear to be definitely homothallic (22). It was of interest, therefore, to look for any evidence as to the condition of sexuality in the lilac strains of *Phytophthora*. Such evidence was easily forthcoming, as an examination showed that in all three strains it was possible definitely to trace the origin of oogonia and antheridia from the same hyphal thread. Such a situation is figured for *Type A* and *P. cactorum* in Figures 29 and 32, 34 respectively, and has been illustrated by Klebahn for *P. Syringae* (18 p. 43, figs, 32, 33). Hence it may be maintained that all three of the strains in question are homothallic, at least customarily.

ABORTIVE REPRODUCTIVE STRUCTURES. Other types of reproductive structures than those considered above have been described

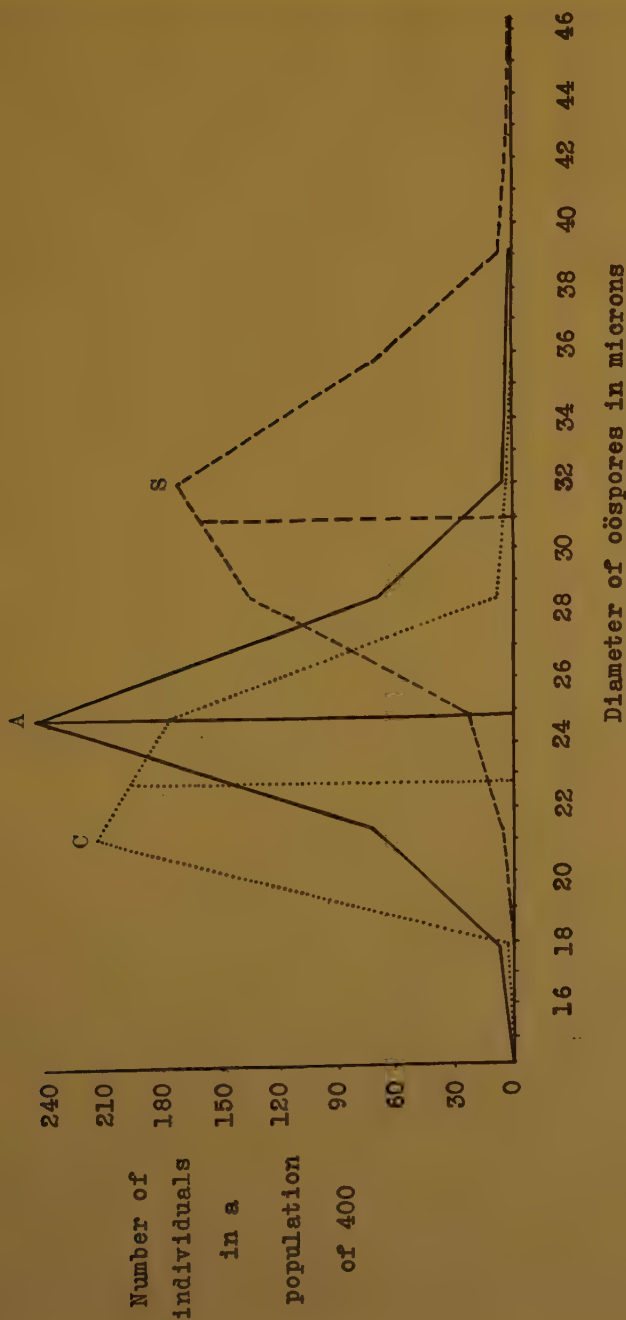


FIG. 1. OOSPORE SIZE IN THE LILAC STRAINS OF PHYTOPHTHORA

KEY: C. = *P. cactorum*; A = *P. cactorum appplanata*; S = *P. Syringae*. The vertical lines represent the positions of the mean diameters.

in *Phytophthora*, as chlamydospores, pseudo-oospores, etc. There appears to be a certain amount of confusion as to the interpretation of these structures. In the strains of *Phytophthora* from Lilac such abortive reproductive structures have frequently been observed. Thus if one applies the Klebs technique to the fungi one finds that before the production of the great majority of sporangia, tentative attempts at sporangium-production end in an abortive fashion. The sporangia swell as in the typical fashion, but instead of maturing as sporangia a hypha continues out of the papilla region, and the sporangium becomes merely a more or less spherical dark swelling on the hypha. Frequently this is repeated several times in succession so that a chain of such swellings come to lie along the hypha. Although these might at first glance be interpreted as chlamydospores, the intermediate stages indicate that they are merely abortive sporangia formed when the conditions for sporangium-production are approached but not quite realized. This phenomenon is particularly noticeable in *P. Syringae*. At other times, particularly in old water cultures of *P. cactorum*, one frequently finds many "oospores" without antheridia. Whether these represent true oospores which have as yet failed to become fertilized, or whether they represent an abortive type of oospore or sporangium cannot readily be answered. Both the "unfertilized oospores" and the abortive sporangia, in any case, seem to be so dependent upon environment for their production and so erratic in occurrence that they are merely mentioned in passing, and no attempt will be made to use them in species distinctions.

C. SYSTEMATIC CONSIDERATIONS

With the background of comparative physiology and morphology as treated above it is now possible to orient the three lilac strains of *Phytophthora* within the genus. Since its original description *P. Syringae* has been felt to represent a well characterized and distinct species. Gäumann (12) considers it a race of *P. omnivora* de Bary, but the form of the sporangia together with other characters easily distinguish it from the *omnivora* group. The cultures of *P. Syringae* studied and reported in this paper conform in every respect to the original and to subsequent descriptions of *P. Syringae*.

Phytophthora cactorum (L. & C.) Schroet. includes a number of other species names according to the conceptions of various workers. Tucker's view of *P. cactorum* (32) includes *P. Fagi* Hartig, *P. omnivora* de Bary, *P. Pini* Leon., and its variety *Antirrhini* Sun. & Ram., and *P. Paeoniae* Coop. & Porter. Various species have been included within the concept of *P. cactorum* by Leonian and others.

No attempt will be made here to determine the species limits of *P. cactorum* in respect to the various allied species of the *cactorum-omnivora* group. Suffice it to say that all of the species so included are characterized by having the prominent type of papilla illustrated in this paper in Figures 9-16. Certainly *P. cactorum* is well distinguished from *P. Syringae*, although both typically have paragynous antheridia, by its prominent papillae and its very different power of growth and reproduction, even at temperatures at which *P. Syringae* utterly fails to make progress. The study of the cultures of *P. cactorum* considered in this paper shows the fungus to be perfectly typical to the earlier descriptions.

Passing then to the third lilac strain, *Type A*, one is confronted with the problem of ascertaining its systematic position. In the type of antheridia and in the majority of its physiological reactions it is manifestly similar to *P. cactorum*. The question then arises as to whether any description has been published of a *Phytophthora* bearing such a combination of characters as those described for *Type A*.

According to the treatment of Tucker (l. c.), the most recent thorough taxonomic treatment of the genus, *Type A* would necessarily fall within the group comprising *P. cactorum* and *P. Syringae* (with widely spreading growth on all ordinary media after 6 days at 20° C., and with predominantly paragynous antheridia). A number of species have been added to the literature since the publication of Tucker's work and these are here briefly considered.

In *Phytophthora gonapodiodes* (Peters.) Buis. (9) the secondary sporangia proliferate through the preceding sporangia in a fashion wholly different from that of any other *Phytophthora* species. *P. Porri* Foister, recently described on the Leek (11), is commonly characterized by apapillate sporangia and paragynous antheridia but it differs from *Type A* in the much larger oospores (32-33 microns) and proportionally much smaller antheridia. The descriptions of four species and varieties recently studied by Sideris have been made available through the kindness of Dr. Sideris (30). None of these, however, are identical with *Type A* since in *P. manzana* Sideris on *Ricinus* the sporangia are stipitate and papillate and sexual organs are absent, in *P. symmetrica* Sideris on *Ficus* the conidia usually germinate by a germ tube, and the sexual apparatus is absent, while in both *P. Meadii* var. *ananaphthora* Sideris and in *P. melongena* var. *ananaphthora* Sideris on *Ananas* the sporangia are prominently papillate and the antheridia predominantly amphigynous. A group of species from Formosa have recently been described by Sawada. Neither of the two species not included in

Tucker's treatment could be identical with *Type A* since in *P. Cyperi-rotundati* Sawada (28) the papillae are flat but the sporangia are pedicellate and the oospores are too large, averaging 30.8 microns, while in *P. Lepironiae* Sawada (= *Nozemia Lepironiae* [Saw.] Saw.) (27) the sporangia are entirely apapillate and the oospores very large, averaging 30–38 microns. *Phytophthora megasperma* Drechs. on *Althaea*, described by Drechsler in 1931 (10a), differs from *Type A* in the internal proliferation of the sporangiophores and in the very large size of the oospores (averaging 41.4 microns). Finally a new strain of *Phytophthora Syringae* has been very recently described by Ogilvie as causing a fruit rot of apples and pears in England and South Wales. This new strain, however, in morphology and in physiological reactions is plainly distinct from *Type A*. Thus Ogilvie records that the growth of this strain is poor or imperceptible on malt agar, bean agar, and corn agar, and that oospores are formed only on Quaker Oat agar, while it has already been pointed out that *Type A* vegetates and forms oospores profusely on these media. Ogilvie's strain also shows on potato-dextrose agar the knotty development of the mycelium so characteristic of *P. Syringae* and only rarely seen in *Type A*.

It is thus seen that *Phytophthora Type A* from Lilac differs strikingly from any described species of *Phytophthora*, while it resembles more closely *P. cactorum* than any other described species. It differs from *P. cactorum* in several respects, chief of which is the flattened nature of the sporangial papilla. It is therefore felt that *Type A* represents if not a distinct species at least a distinct variety of *P. cactorum*, and accordingly it is here so indicated. Since the structure of the papilla is the most striking differential character in comparison with *P. cactorum*, the name *Phytophthora cactorum* (L. & C.) Schroet. var. *applanata* n. var. is proposed. The diagnosis of this variety is here introduced.

Phytophthora cactorum (L. & C.) Schroet. var. *applanata*, n. var.

A typo differt sporangii papillis applanatis non prominentibus.

This variety differs from the species in the consistent presence of flattened, non-prominent sporangial papillae. Parasitic on the young growth of various horticultural varieties of *Syringa vulgaris* causing a soft dark decay. Hab. in Massachusetts, U. S. A.

V. COMPARATIVE PATHOLOGY OF THE SPECIES OF PHYTOPHTHORA PARASITIZING LILAC

Having inquired into the structure and behavior of the lilac strains of *Phytophthora* and established their identity, it now becomes necessary to consider more in detail the diseases caused by

them. The present section, accordingly, will deal with the nature of the diseases caused, reserving for the following section a treatment of the subjects of prognosis and control. The nature of the diseases of Lilac caused by *Phytophthora* species has been ascertained both by observations of the symptoms and of predisposing factors to the diseases as they occur in the field and also by infection experiments. These sources of evidence will accordingly be treated in turn. It must be stated at the outset that the disease caused by *P. Syringae* does not appear to occur in America, and accordingly the description of this disease is based upon the fairly extensive published accounts.

A. SYMPTOMS

According to Klebahn (18) the disease caused by *Phytophthora Syringae* manifests itself first by an inhibition of development of the buds of the younger shoots. The cortex of the diseased twigs is killed with the result that the bark of the diseased twigs is darker than that of healthy twigs and somewhat shrunken. Usually such killing of the cortex involves the whole circumference of the twigs. The vascular system is not affected in the earlier stages of the disease but eventually it becomes interfered with and the whole of the affected twig dies. Occasionally the disease may be limited to a single bud or part of a bud. Such symptoms become noticeable only at the time of spring development, although the fungus may be actively killing the cortex during the winter.

Miss de Bruyn has pointed out (6) that *Phytophthora Syringae* may also attack the leaves, causing irregular brown patches with lighter margins. If the *Ovularia Syringae* of Berkeley is the same fungus as *Phytophthora Syringae* (Kleb.) Kleb., as is probable, then Berkeley's description of the brown leaf infections of lilac (4) harmonizes with the findings of Miss de Bruyn. Arnaud has also observed the same type of leaf infections (1, 2). Oospores are customarily found in the infected tissues, and in moist weather zoosporangia are also produced, the latter emerging through the stomata as in the case of *Phytophthora infestans* according to Berkeley. Finally the infection experiments carried out in connection with the study reported in the present paper indicate that *Phytophthora Syringae* is also able, under some conditions, to attack the succulent young tissues in the same fashion as is characteristic of the other two lilac strains of *Phytophthora*.

According to White's description (35) the infection caused by *Phytophthora cactorum* takes place in the succulent young shoots. "A die-back condition is caused by the invasion of the fungus in the cortex of the shoot, and in some cases suckers three and four feet

long have been killed to the ground. Frequently the entire crop of root suckers which arise about the base of old lilac bushes have been completely killed. On leaves, infections first appear as small, water-soaked areas, increasing in size during periods of rain, but drying out during periods of dry weather. Entire leaves may be invaded, and the fungus has been found growing down the petioles into the cortex of the branch where dark brown or black cankers are produced."

The disease observed in Boston follows in general the same course as that in New Jersey. Infections of the young shoots are observed soon after the buds have started development, and the disease is maintained through the summer months in the supply of soft young suckers which are constantly being formed at the bases of older lilac plants. Hardening of the wood completely checks the disease provided it has not advanced too far for the recovery of the shoot. The stem lesions appear to be more frequent, somewhat resembling those caused by *Bacterium Syringae* in being elongated, dark, and soft, but becoming hard and calloused in the cases where the shoots recover. Oospores are frequent in the diseased tissues, and sporangia are produced on the surfaces of the lesions during moist weather or if the lesions are placed in moist chambers.

The disease caused by *Phytophthora cactorum* var. *applanata* in all essential features resembles that caused by *P. cactorum*, so much so that no additional description is necessary, the lesions being confined to the succulent tissues, being dark, soft, and elongate, and becoming checked by the hardening of the tissues affected.

B. PREDISPOSING FACTORS

Phytophthora Syringae, as may be seen from the work on temperature relations of the fungi, is an organism favored by cool weather. It was noted above that its growth ceases at 25° C. (77° F.), and as this temperature is frequently exceeded in the spring and summer months it is not surprising to find that the disease caused by *P. Syringae* is essentially a disease of winter and early spring. Klebahn (18) found the disease to be primarily one of plants which had been closely packed in cool chambers for the winter and covered with leaves preparatory to forcing in the spring. Miss de Bruyn (6), in investigating more accurately the relation between season of the year and occurrence of the disease, found that a maximum number of successful stem inoculations could be made in November, the number decreasing to practically zero in the summer, and again increasing in the fall. The same was true of bud inoculations which reached a percentage of successful inoculations of 100% in Novem-

ber and December and fell to 0% in September. Moreover, she also reported that the increase in length of stem inoculations was greatest in February, falling to zero in July and again beginning a gradual increase in November.

On the contrary the other two *Phytophthora* strains causing lilac disease are fungi favored by higher temperatures. Accordingly it is consistent that the lesions caused by the latter are more prevalent during the spring and summer months and are absent during the winter.

Moisture plays an important role in the severity of all of the *Phytophthora* diseases of Lilac. Spread of the diseases in all cases is chiefly through the activity of the zoospores, the oospores being non-motile and buried within the tissues, to be freed only by the disintegration of the diseased parts. A high degree of humidity is essential to the production of sporangia, and water is necessary for the life and distribution of the zoospores. Therefore the rate of spread of the diseases is conditioned by the rainfall and humidity. Herein lies one reason for the destructiveness of the disease caused by *Phytophthora Syringae* in the European forcing beds. The plants which had been stored were covered with a moisture retaining layer of leaves which greatly facilitated the dispersal by zoospores. The increase in size of *P. cactorum* lesions in periods of rain has been noted above, and White has also observed that excessive shade and relatively high humidity are conducive to the spread of the disease caused by *P. cactorum*. Excessive rainfall also exerts a secondary influence upon the severity of the diseases caused by *P. cactorum* and its variety *applanata*. It is a matter of frequent observation that prolonged rainy seasons prolong the period before the new growth begins to harden. Accordingly, as the period of succulence is extended the opportunity for infection and enlargement of the lesions becomes proportionally increased. In the case of the disease caused by *P. Syringae*, rainfall has still another unfavorable influence. Miss de Bruyn has observed (6, 7) that during seasons with abnormal rainfall in August and September the development of the fungus concerned upon the leaves is greatly aided while leaf fall is retarded. The development of the fungus becomes sufficient, under such circumstances, that the fungus can pass down the petioles and into the cortex of the stems, thus establishing itself in the woody tissue and offering a source of infection for spread during the winter months.

As another predisposing factor should be mentioned the methods of planting and of cultivation. If Lilacs are so heeled in that the buds come to lie in proximity to the soil they are in a favorable

situation for infection, since *Phytophthora* species are able to exist saprophytically in the soil. Such a method of planting is frequently employed, and Klebahn called attention to the destructiveness of the infection by *P. Syringae* resulting. Lustner (24) observed that of two similar groups of Lilacs, one of which had been planted in normal fashion, the other heeled in, only the latter group suffered from the disease caused by *P. Syringae*. In the case of the diseases due to *P. cactorum* and *P. cactorum applanata* the method of cultivation may likewise exert an influence upon the severity of the disease. As it has been shown above that these diseases are maintained during the summer upon the succulent young suckers at the bases of old lilac plants, it is manifest that clean cultivation involving the continual removal of such suckers will decrease by much the amount of inoculum available the following spring. Such suckers improve neither the appearance nor the health of mature specimen Lilacs, and clean cultivation is hence doubly desirable.

A fourth predisposing factor may be injury. Klebahn was unsuccessful in causing infection with *P. Syringae* to woody stems unless these had been previously injured, and accordingly it is probable that infection in nature is facilitated by injuries. However, in the cases of the diseases caused by the other two lilac strains of *Phytophthora*, infection of the succulent growth appears to be independent of injury.

C. INFECTION EXPERIMENTS

In 1906 Klebahn succeeded in transmitting the disease caused by *P. Syringae* from Lilac to Lilac by means of pieces of infected cortex inserted into healthy lilac stems (17). In 1909 he reported a more extensive series of infection experiments using pure cultures of the fungus (18). He was able to secure satisfactory infections in wounds in the woody stems as well as in uninjured buds using mycelium as the inoculum, and likewise to infect successfully using pure cultures of swarm spores. He also carried out a series of infection experiments demonstrating that the fungus was not only able to infect Lilac but that it would likewise infect a variety of other related and unrelated hosts such as *Jasminum*, *Forsythia*, *Crataegus*, *Pyrus*, *Prunus*, *Acer*, *Aesculus*, *Alnus*, *Corylus*, *Quercus*, and *Tilia*. Negative results were obtained with a number of other inoculated subjects.

De Bruyn's inoculation experiments with the same fungus (6) have already been mentioned. It will be recalled that she was able to obtain a high percentage of infections on lilac during the winter, using mycelium as inoculum. The only other infection experiments with *Phytophthora* from Lilac are those of White in 1929 with *P.*

cactorum. White mentions (35) that he has successfully performed repeated cross inoculations with this organism between Lilac and Rhododendron, which latter is also parasitized by *P. cactorum* in nature.

During 1930 and 1931 a number of infection experiments were performed by the writer with all three strains of *Phytophthora* from Lilac. These will be summarized at this point.

On April 2, 1930 ten pot plants of *Syringa vulgaris* var. *purpurea* with stems of 1 cm. diameter were inoculated in knife wounds of the woody stems with mycelium from agar cultures of *Phytophthora Syringae*. The inoculations were bound with wet sphagnum and raffia in the conventional manner and placed in a large moist chamber. On examination five months later all the inoculations were negative. The failure was probably due to the time of year of inoculation since Miss de Bruyn likewise obtained almost negative results in inoculations performed in April.

The same experiment was repeated the following December using 24 similar host subjects and inoculating eight each with *P. Syringae*, *P. cactorum*, and *P. cactorum* var. *applanata*, respectively. The inoculations were performed as in the preceding experiment except that in some of the plants semi-woody tissues were inoculated, while in other plants only the woody stems were employed. The extent of spread of the lesions was observed three months later. The following table gives the results.

AVERAGE INCREASE IN SIZE OF LESIONS (mm.)			
INOCULATION IN	P. SYRINGAE	P. CACTORUM	P. CACTORUM APPLANATA
Hard wood.....	23.0	17.2	17.6
Semi-woody tissues.....	1.2	4.0	3.0

The respective fungi were reisolated from the margins of the majority of the lesions three months after inoculation. The results indicate that although *P. Syringae* is most virulent in woody tissues, *P. cactorum* and *P. cactorum applanata* can also cause infection in such tissues. Since the inoculated plants were in a greenhouse the temperature of which was moderately high, *P. cactorum* and *P. cactorum applanata* were growing at a temperature favorable for their development and one which would not obtain at this season in nature.

A third infection experiment was performed in April, 1931, differing from the preceding in that the normal succulent growth was selected as the infection court. The inoculum was in the form of pure cultures of the three lilac strains of *Phytophthora* on agar. In some subjects a pair of leaves was removed from each succulent

shoot and the inoculum bound over the leaf scars, in others no injury was resorted to. The inoculations were then surrounded with moist cotton and raffia and placed in moist chambers. Five plants each were used for each strain of fungus. The results were as follows:

HOST INOCU- LATED	ORGAN INOCU- LATED	P. SYRINGAE		P. CACTORUM		P. CACTORUM APPLANATA	
		INOCUL'S	INFECT'S	INOCUL'S	INFECT'S	INOCUL'S	INFECT'S
<i>Syringa</i> <i>vulgaris</i>	Succulent shoots	14	(2) (Very weak)	30	28	15	6
<i>Syringa</i> <i>vulgaris</i>	Blossoms					1	1
<i>Ligustrum</i> <i>ovalifolium</i>	Succulent shoots			12	2	8	(1)
<i>Ligustrum</i> <i>ibota</i>	Succulent shoots			2	0	2	(Very weak) 0

In a number of instances in the infections with *P. cactorum* and *P. cactorum applanata* there was clear-cut evidence from the limits of the infections produced that the respective fungi had succeeded in penetrating through the uninjured epidermis. This experiment indicates that under more nearly natural conditions in the spring *P. cactorum* is highly virulent to succulent lilac tissues, *P. cactorum* var. *applanata* somewhat less so, and *P. Syringae* very weakly aggressive.

In the typical negative inoculations with *P. Syringae* indicated in the table there was frequently a small brown area marking the original entry of the fungus, but around this developed a layer of callus tissue, cutting off the lesion from the rest of the stem tissue. With the employment of *P. cactorum* and *P. cactorum* var. *applanata* the typical lesion took the form of a brown, soft area which appeared within 48 hours of the time of inoculation. Such brown areas were not necessarily restricted to injured points on the shoot. From the brown area watery streaks extended up and down the stem, looking as though the cells of the streaks had been mechanically crushed. Very rapidly these streaks turned brown and soft until the advance involved several centimeters after 96 hours. The shoots would then fall over at the rotted part and the distal portions would die. Cut leaf bases were readily occupied by both the fungi, but there was a partial checking of fungus growth at the layer of abscission, that is, the fungus appeared to pass that layer with some difficulty. The lesions were usually covered with *Phytophthora* mycelium when removed from the moist chamber.

The evidence from the preceding experiment shows that under some conditions *P. Syringae* is able weakly to infect succulent lilac tissues. In order to test this matter further, however, an experiment was set up in April 1931, using zoospores as inoculum. Glass

collars were fitted around the stems of 15 pot lilacs (*Syringa vulgaris purpurea*) each with a succulent shoot at the top of the stem and partly within the glass collar. The glass collars were fashioned and sealed in the manner described by Klebahn (18). Into the collars of ten of the plants were then poured pure cultures of freshly liberated zoospores of *P. Syringae*. The remaining 5 plants were similarly treated but using sterile water instead of the zoospore suspensions. The following day a second dose was given to 8 of the experimental plants and to four of the controls. The day after a third dose was given to 6 of the 8 mentioned above and to 3 of the controls. This process was repeated until the last two of the experimental plants had received 5 daily doses of the zoospore culture and the last control 5 doses of sterile water. The plants were later examined for infection. The results of the examination are given in the following table:

NUMBER OF DAYS OF TREATMENT	TREATED WITH	
	PURE CULTURE OF ZOOSPORES OF <i>P. SYRINGAE</i>	STERILE WATER (CONTROL)
1	Slight infection	No injury
2	Typical infection	Slight browning
3	Typical infection	No injury
4	Typical infection	No injury
5	Typical infection	Slight browning

This experiment therefore, indicates that although *P. Syringae* is primarily a fungus causing disease in woody tissues of Lilac and in the winter, nevertheless, it is able under some conditions to cause an infection of succulent tissues in a manner similar to *P. cactorum* and *P. cactorum applanata*.

Summarizing the results of all the infection experiments performed to date with the lilac Phytophthoras, one can say that *P. Syringae* has been shown to be capable of causing infection in injured woody stems during the winter months but not during the summer months, in uninjured buds during the winter months, and in more succulent tissues under certain conditions in the spring and summer. However, it is primarily a parasite of dormant tissues. *P. cactorum* and *P. cactorum* var. *applanata*, on the contrary, have been proved to be more readily capable of causing disease in succulent tissues during the spring and summer than *P. Syringae*. On the other hand, although these latter fungi are also capable of parasitizing dormant tissues, they are less aggressive in such tissues than *P. Syringae*. The inoculation experiments thus confirm the observations that in nature *P. Syringae* is primarily the cause of a disease of dormant Lilacs, *P. cactorum* and its variety *applanata* primarily the causes of diseases of succulent young sprouts.

VI. PROGNOSIS AND CONTROL

The final chapter of such a study as the present one, and from the practical standpoint the most important one, necessarily must be concerned with the control of the diseases in question. However, before proceeding directly to the question of control it is advisable to consider briefly the conditions under which the diseases are likely to be most severe and to warrant active steps in control.

The *Phytophthora* diseases of Lilac under ordinary conditions are not as destructive as are many of the more devastating diseases of other economic plants. There is little likelihood of their increasing to epidemic proportions, at least under American conditions of lilac culture. On the other hand, given optima of moisture, temperature, and supply of inoculum, the diseases may well merit serious measures for control. This fact is particularly true of an ornamental plant such as the Lilac where infections of a severity which would not seriously diminish the quantity of product in crop plants, may in ornamental plants, nevertheless, diminish very appreciably the market or aesthetic value of the host.

The disease caused by *P. Syringae* in the European lilac forcing industry as well as in nurseries and private collections has already shown itself capable of warranting prophylactic measures. This has been particularly true in seasons in which there has been an abundance of rain in August and September and under cultural methods which facilitate the development of the lesions and the spread of inoculum. Such methods are those by which Lilacs are closely packed in relatively air-tight chambers, preparatory to shipment, transplantation, grafting, or forcing. On the other hand, where Lilacs are well spaced, growing under more or less natural conditions outdoors in the private collection or nursery, the spread of the disease is much less readily accomplished, and control by natural agencies will probably be relatively effective.

As regards the other diseases caused by *Phytophthora cactorum* and *P. cactorum* var. *applanata*, the conditions favoring the diseases are somewhat different. Here the diseases are more likely to become epidemic in natural plantings, particularly during those seasons in which the spring rains are prolonged. Moreover, as spring is the season of the year during which the Lilac attracts most attention, infections in the foliage and blossoms in the spring are doubly important. Hence it will be seen that the latter diseases may at times be rather important under American conditions of lilac culture. It certainly will be to the advantage of the lilac grower to examine his plants during early spring and up to blossoming time for *Phytophthora* infections, especially during the more rainy seasons, and to

take prompt steps to check any serious impending spread of infection.

The methods of prophylaxis against a *Phytophthora* disease in Lilac depend upon the species of *Phytophthora* involved. Control of the European disease, caused by *P. Syringae*, has been worked at rather at length by both Klebahn and de Bruyn. Klebahn's suggestions (18) include the removal and burning of all infected plant parts, cultural methods which eliminate the close heeling-in of stored Lilacs, maintenance of a low degree of humidity in stored lilacs especially by elimination of leaves as a covering for such plants, and finally avoidance of mechanical injuries to the Lilacs by careful cultural practices. After a few years of observance of such suggestions, Klebahn felt that the disease had been somewhat diminished in frequency. He suggested that fungicides, used during storing and eventually in the nursery, might be of value, but he did not test their efficacy. Miss de Bruyn (6) originally added to Klebahn's suggestions the desirability of removing the infected leaves by hand during such years as show an abnormal rainfall in August and September, but a later study (8) showed that the quality of the blooms was so decreased by such treatment that the method was not considered advisable. She also suggested Bordeaux and lime-sulphur sprays, cautioning at the same time against spray injury to the young tissues.

As regards the other *Phytophthora* diseases of Lilac, the experimental conditions have not been favorable to a thorough comparison of control measures. However, a knowledge of the success of prophylactic treatments in diseases caused by similar fungi and of the physiology of the fungi involved here leads one to a number of *a priori* suggestions. White's recommendations for the control of the disease caused by *P. cactorum* (35) embody avoidance of planting of Lilacs near to Rhododendrons (since the fungus involved also parasitizes Rhododendron), removal and burning of dead wood, soil sterilization where practicable, discreet pruning, and spraying with a dormant application of lime-sulphur together with summer applications of Bordeaux.

In the control of both of the latter diseases good cultural methods should prove most useful. The ideal Lilac, according to most growers, is a single-stemmed plant of the general form of an inverted cone. An abundant crop of suckers at the base detracts both from the aesthetic value of a plant and from its ability to blossom. Moreover, it is the suckers which materially aid in carrying the infection through the summer. Hence the complete and regular removal of such suckers is to be advocated. Combined with this, care should

be taken to keep the bushes properly spaced and thinned out in order to avoid excess of moisture and shade. During the spring, particularly during wet seasons, frequent examinations should be made for *Phytophthora* lesions on the young growth, and if such lesions are found they should be immediately destroyed. If lesions occur to a considerable extent on the shrubs, protective applications of Bordeaux are indicated, and without delay, since the spread of the diseases is very rapid under such conditions. It has been suggested that the spotting caused by the Bordeaux may be deleterious to the appearance of the plants. Such an objection would not apply to the nursery, but in private collections the spotting might be avoided by the substitution of one of the non-spotting fungicides now on the market. Methods of soil sterilization for the most part could not be conveniently applied to standing lilacs, but under the conditions of some propagation practices it would be well to consider soil sterilization in case of a severe attack by *Phytophthora cactorum* or *P. cactorum applanata* on nursery stock.

The efficacy of Bordeaux spray and sulphur dust as protective agents were investigated in the following manner. Water cultures of the three *Phytophthora* strains were prepared in order to obtain suspensions of freshly liberated zoospores. Drops of the zoospore suspensions of each fungus were then placed on microscope slides which had been in one case dusted with a reputable commercial sulphur dust, in a second case sprayed with a 4-5-50 Bordeaux mixture, and in the third case untreated. Examinations were first made for loss of motility of the zoospores. It was found that with *P. Syringae* the untreated spores remained active for about an hour, the Bordeaux treated spores lost all motion within 5-10 minutes, and the sulphur treated spores lost all motion in about 20 minutes. With the spores of *P. cactorum* the controls remained active for nearly an hour, and those treated with Bordeaux and sulphur for 10-20 minutes. With *P. cactorum applanata* the controls remained active for nearly an hour but all motion was lost in the spores treated with both Bordeaux and sulphur in less than 5 minutes.

As regards germination, the control spores of *P. Syringae* germinated to an extent of about 90% in 24 hours, those of *P. cactorum* to about 99%, and those of *P. cactorum applanata* to about 80%. Meanwhile the Bordeaux treated spores of all three strains completely failed to germinate, while the sulphur treated spores germinated in *P. Syringae* 85%, in *P. cactorum* 77%, and in *P. cactorum applanata* 70%.

This experiment accordingly indicates that Bordeaux of a strength of 4-5-50 will completely inhibit zoospore germination in all the

lilac strains of *Phytophthora*. Hence in the field one would anticipate that Bordeaux would offer a very satisfactory protection, since infection in the field is apparently almost or quite exclusively by zoospores. On the other hand, sulphur dusting would not be expected to give satisfactory results since it exerts very little inhibiting effect upon zoospore germination.

VII. SUMMARY

1. The present paper reports a comparative study of three strains of *Phytophthora* parasitizing Lilac, and of the diseases caused by them. The fungi involved are *Phytophthora Syringae* (Kleb.) Kleb., *P. cactorum* (L. & C.) Schroet., and a third strain here tentatively referred to as *Type A*.

2. The physiological behavior of the three strains of *Phytophthora* was investigated with the following results:

a. In regard to rate and type of growth upon a variety of artificial substrata, *Phytophthora Syringae* was found to differ markedly in its reactions from the other two strains, while the latter, although in general similar to each other, showed certain suggestive differences.

b. With respect to production of reproductive organs upon a variety of artificial media, *P. Syringae* again proved to be entirely distinct, while certain minor differences distinguished *P. cactorum* and *Type A*.

c. In relation to temperature, *P. cactorum* and *Type A* were found to vegetate luxuriantly at temperatures as high as 25° C, at which temperature *P. Syringae* failed to make any growth. The optimum temperature for the former two strains was found to be in the neighborhood of 25° C., in contrast to 20° C. for *P. Syringae*.

d. The strains manifested corresponding differences with regard to pH. *P. Syringae* vegetated well between pH 3.5 and 7.0, growth virtually ceasing at 7.5, *P. cactorum* showed good growth in the very long range from 3.0 to 10.0, while *Type A* grew satisfactorily between 3.0 and 9.5. In passing, the subject of vital staining of the lilac strains of *Phytophthora* was investigated. Staining of the vacuoles was observed with neutral red but not with methyl red, indicating that the vacuoles of these strains of *Phytophthora* are of the type designated by Bailey as Type B. Methyl red was not reduced by *P. Syringae* but was reduced by the other two strains. The oospore walls of *P. cactorum* and *Type A* were brilliantly stained *in vivo* by a number of the stains employed.

3. The morphology of the three strains of *Phytophthora* was likewise investigated with the following results.

a. Minor, but no important differences were observed in the mycelial characters of the three strains.

b. The sporangia differed markedly with respect to the type of papilla of zoospore emergence. That of *P. cactorum* was strikingly different from those of *P. Syringae* and *Type A* in being very prominent, in contrast to the flattened, inconspicuous papillae of the other strains. This character was striking and constant, and was the most useful criterion for distinguishing the otherwise similar *P. cactorum* and *Type A*.

c. Few significant differences were observed in the sexual apparatus of the three strains. The antheridia were mainly paragynous and the mycelia homothallic in all the strains. There was, however, a significant difference in oospore size between *P. Syringae* and the other two strains.

d. Abortive reproductive structures are discussed as they occur in the three strains.

4. On the basis of the work on the comparative physiology and morphology of the three strains, their respective systematic positions are discussed. *Type A* was found to resemble *P. cactorum* more closely than any other species of the genus. However its different form of papilla, together with other more minor differences, have lead to its recognition as a new variety of *P. cactorum*, namely *P. cactorum* var. *applanata*, n. var., the diagnosis of which is given.

5. The comparative pathology of the three lilac strains of *Phytophthora* was investigated. *P. Syringae* was found to differ markedly from the other strains in the type of lesion produced, the tissues attacked, and the time of year of greatest fungus activity. *P. cactorum* and *P. cactorum* var. *applanata* behaved in a similar fashion pathologically. The symptoms caused in Lilac by the three strains of *Phytophthora* are described, the factors predisposing to the diseases caused are analyzed, and the pathogenicity of the three strains under various conditions determined by infection experiments.

6. On the basis of the comparative study of the fungi and of the diseases caused by them, the probable severity of the diseases is discussed, together with the conditions under which the diseases are likely to prove most destructive. Finally the possible methods for the control of the diseases are considered and recommendations made as to the prophylactic practices found desirable.

VIII. ACKNOWLEDGEMENT

The study herein reported has been materially aided by the suggestions of Professor J. H. Faull to whom I wish to express my

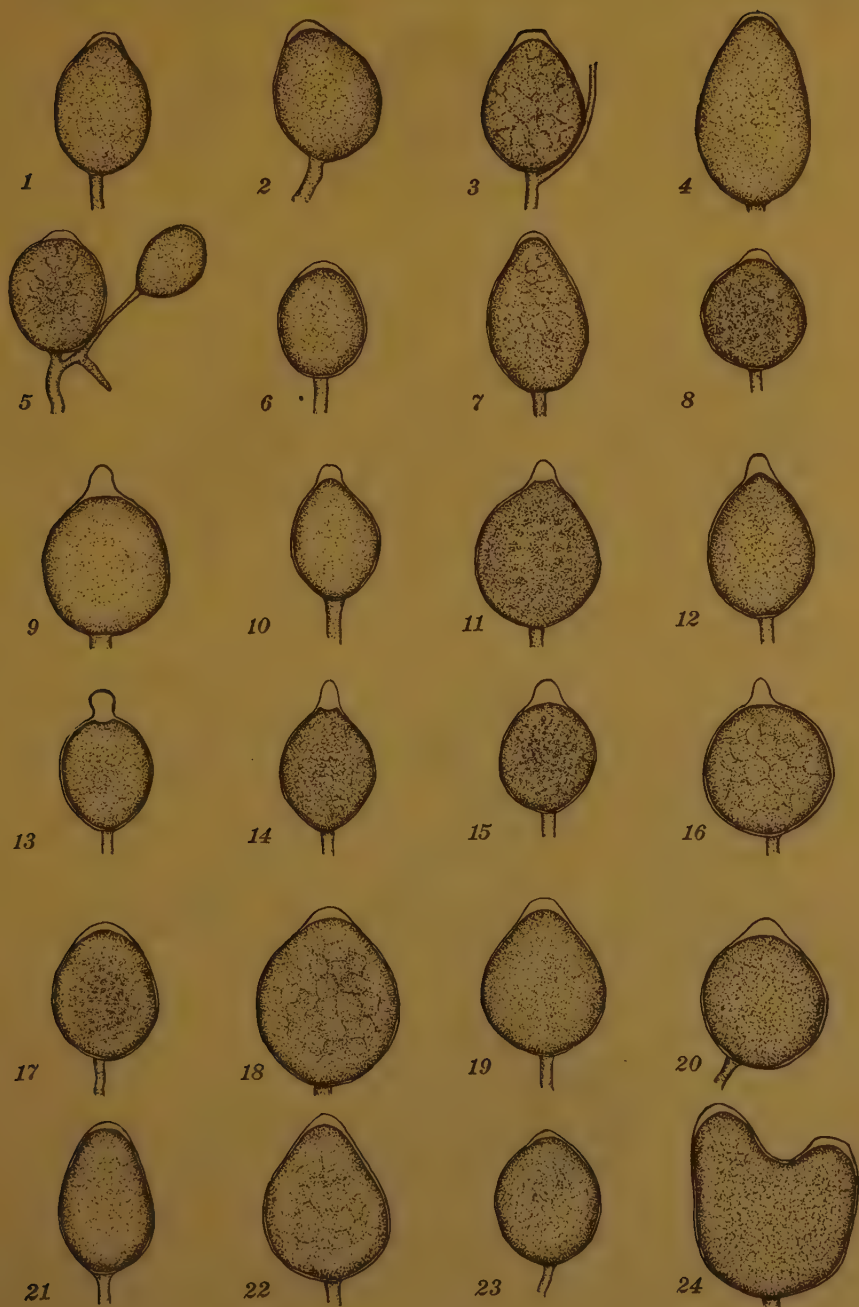
thanks. Acknowledgement is also due to Professor I. W. Bailey for suggestions regarding the experiments in staining *in vivo*.

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PHYTOPHTHORA DISEASES OF LILAC



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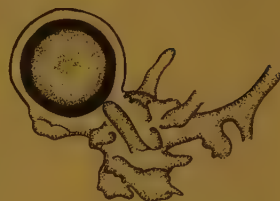
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PHYTOPHTHORA DISEASES OF LILAC

EXPLANATION OF PLATES 46 AND 47

- Figs. 1-24. Sporangia of the lilac strains of *Phytophthora*. Camera lucida drawings from living material. $\times 1000$.
- Fig. 1-8. *Phytophthora Syringae*. Typical sporangia illustrating the general structure and flattened type of papilla.
- Fig. 9-16. *P. cactorum*. Typical sporangia illustrating the prominent type of papilla characterizing this species.
- Fig. 17-24. *P. cactorum* var. *applanata*. Typical sporangia except for Fig. 24 which represents a bicornute abortive type frequent in old water cultures. Illustrative of the flattened papilla which differentiates this variety from *P. cactorum*. Fig. 20 represents as well developed a papilla as has been seen in this variety, the majority of the sporangia in cultures of *P. cactorum applanata* being of the form indicated in Figs. 17, 18, 21, and 22.
- Figs. 25-34. Sexual reproductive organs of the lilac strains of *Phytophthora*. Camera lucida drawings from living material. $\times 500$.
- Fig. 25, 26. *P. Syringae*. Fig. 25, oogonium; Fig. 26, oospore. Showing the typical basally paragynous antheridia.
- Fig. 27-30. *P. cactorum* var. *applanata*. Figs. 27, 29, oogonia; Figs. 28, 30, oospores. Illustrating in Fig. 29 the homothallic nature of the vegetative body and in Fig. 30 the highly proliferate type of antheridium frequently found in old cultures.
- Fig. 31-34. *P. cactorum*. Oospores. Figs. 32 and 34 demonstrate the heterothallic nature of the mycelium, while the typical basally paragynous antheridia are best evident in Figs. 31 and 33.

PARASITISM OF MYXOMYCETE PLASMODIA ON THE SPOROPHORES OF HYMENOMYCETES

FRANK L. HOWARD AND MARY E. CURRIE

With plates 48 and 49 and two text figures

THE interest of authors was aroused in the subject of the parasitism of Myxomycetes when they found plasmodia creeping over and destroying the fruitbodies of mushrooms and polypores in the forests. Because Myxomycetes are usually found on decaying wood, dead leaves, and other organic debris, the notion is current that their nourishment is derived chiefly from the bacterial and fungous decomposition of these substrata. Even though myxomycetous sporangia are occasionally found on disintegrating fructifications of polypores, mushrooms, and other fungi in the forests, collectors rarely conceive of the disintegration observed as being due to the plasmodia from which the sporangia are formed. There are students of the Myxomycetes, however, who have been impressed by the possibility of their active parasitism on fungi, as is pointed out in our résumé of the literature. The authors of the present paper have independently made extensive observations on the mycophagy of the slime molds in the field and supplemented them with tests in the laboratory. The results, dealing with the nutritional relationships of a considerable number of the Myxomycetes to the sporophores of fungi, and the process by which the plasmodia digest the fungal tissues, are presented here.

The general method used to obtain plasmodia for this study was, either to collect them upon Hymenomycetes or other substrata and to bring them into the laboratory, or to grow them from spores in culture upon suitable nutrient agar media. During the season when mushrooms were available, as many different kinds as possible were gathered, identified, and placed in large petri or-crystallizing dishes lined with moist filter paper or paper toweling. The sporophores were inoculated by placing a piece of plasmodium varying from 0.5 to 2.5 sq. cm. in area upon the apex of the stipe of stipitate fruitbodies or at the base of sessile forms. Notes were taken daily upon the virulence of the attack and the nature and extent of the tissues of the host being digested. Details of the process of destruction of the fungous tissues were obtained, either from microscopic examination of living material, or from examination of material fixed in Navaschin's, Bouin's, or chrom-acetic solution,

cut into sections $3\ \mu$ to $10\ \mu$ thick after embedding in paraffin, and stained with Flemming's triple or with iron-alum-haematoxylin.

The observations reported in this paper are the result of two independent investigations upon this subject. The junior author, now Mrs. Gordon Edwards, carried on her work as a graduate student in the Botanical Laboratories of the University of Toronto, during the years 1919-1921, under the direction of Professor J. H. Faull, now Professor of Forest Pathology at the Arnold Arboretum, Harvard University. The observations contributed by the senior author were made at Harvard University under the sponsorship of Professor W. H. Weston, Jr., during the tenure of a National Research Fellowship in the Biological Sciences, 1930-1931.

REVIEW OF THE LITERATURE

The literature contains several references to plasmodia attacking Hymenomycetes which indicate that mycophagy is not uncommon among the Myxomycetes. For the first reference to their parasitism we must look to A. Lister (8), who in January 1877 was led to investigate the parasitism of fungi by the Myxogastrales upon finding *Corticium puteanum* fruitbodies being consumed by a plasmodium of *Badhamia utricularis*. He kept this plasmodium in culture by feeding it sporophores of several species of Basidiomycetes, and although he found that the plasmodium could make use of the majority of these, it showed preferences. In some cases almost the entire fruitbodies were assimilated but in others merely the soft superficial tissues were used. The Myxomycete flourished on *Corticium puteanum*, *Polyporus versicolor*, *P. adustus*, *Merulius* sp., and *Daedalea* sp.; was most luxuriant on *Stereum hirsutum*; rapidly consumed *Boletus flavus* and *Agaricus* (*Psalliota*) *campestris*; slowly attacked *Agaricus* (*Armillaria*) *melleus*; and with great difficulty attacked *Agaricus* (*Amanita*) *rubescens* and *Agaricus* (*Hypholoma*) *fascicularis*. Lister observed that the decomposition products of the attacked fungi many times had a deleterious effect on the plasmodium. He noticed also that there was usually a heavy mucus-like residue which varied in amount with the species of Basidiomycete and in which Mucors and other fungi were apt to grow. He made a microscopic examination of the plasmodium attacking hyphae of *Stereum hirsutum* and found that the threads dissolved and broke in pieces as the hyaloplasm advanced over them.

Blytt (1) in 1879 collected the type of *Clastoderma Debaryanum* on a dead *Polyporus* sp., and Brunaud (2) in 1890 reported finding sporangia of *Enerthenema papillatum* on the debris of a *Corticium*,

Fuligo septica on the pileus and hymenium of a Polypore, and *Stemonitis fusca* on the debris of *Polyporus versicolor*, but neither observer suggests that these Myxomycetes may be parasitic upon the fungi concerned. Likewise, Jahn (7) reports Möller as finding *Trichamphora pezizoides* fruiting on a pileus of *Lentinus villosus*.

Macbride (9) reported the second recognized case of a mycophagous myxomycete when he found that the plasmodium of *Physarum polycephalum* would rapidly digest sporophores of *Agaricus (Pleurotus) sapidus*.

Harshberger (6) shortly afterwards discovered a bright yellow plasmodium attacking *Pleurotus sapidus* sporophores in the field. Upon bringing the plasmodium, which he named *Fuligo septica*, into the laboratory he found that it would attack and digest pieces of *Coprinus comatus*, *C. atramentarius*, *Hypholoma perplexum* and the gleba but not the stipe of *Phallus impudicus*.

Atkinson in 1916 presented a paper before the Mycological section of the Botanical Society of America upon a slime mold parasitic on mushrooms, which was believed to be a *Badhamia*, but this paper has never been published.

Elliott (4) collected further data regarding the action of *Badhamia utricularis* on fungous tissues. He noted the same discrimination for various species of mushrooms as that described by Lister (8). Elliott experimented with *B. utricularis* on *Polystictus versicolor*, *P. hirsutus*, *Polyporus dryadeus*, *Amanitopsis vaginata*, *Amanita rubescens*, *Collybia dryophila*, *Coprinus micaceus*, *Laccaria (Clitocybe) laccata*, *Marasmius oreades*, *Panus stipticus*, *Psilocybe semilanceata*, *Russula furcata*, *R. rubra*, *R. emetica*, *Stropharia semiglobata*, *Boletus scaber*, *B. flavus*, and *Lycoperdon gemmatum*. Elliott observed that unless the plasmodium is able to move away from its host after the decomposition of the fungus sets in, it is killed. In conclusion, he writes that the plasmodium of *Badhamia utricularis* can assimilate nearly all of the fleshy fungi whether poisonous or otherwise. In a later paper with Jessie S. Elliott (5) he describes the sequence of fungi and Myxomycetes upon a large oak branch subsequent to its fall in 1912. Fruitbodies of *Bulgaria polymorpha*, *Coryne sarcoides*, *Stereum hirsutum*, *Panus stipticus*, and *Hypholoma fascicularis (H. fasciculare)* appeared in order upon the branch, but only those of *H. fasciculare* and *S. hirsutum* were in evidence in 1919 when the first Myxomycete, *Physarum nutans* Pers., made its appearance. Sporophores of *Phlebia merismoides*, *Hypholoma sublateralitium* and one of *Pluteus cervinus* were new additions before other crops of *Physarum nutans* appeared in June 1920. In July 1920 the white plasmodium of *Stemonitis*

fusca emerged from the branch but nothing is said regarding its parasitism. The complete disappearance of *Bulgaria polymorpha* and *Coryne sarcoides* is attributed to the destruction and absorption of their mycelia within the wood by *Physarum nutans*.

Currie (3) in 1919, besides reporting *Badhamia utricularis* and *Physarum polycephalum* to be mycophagous, added three more species to our list of Myxomycetes which parasitise fungi, namely: *Badhamia foliicola* List., *B. magna* Peck, and *Physarum flavicomum* Berk.

Sanderson (11, 12) further supplemented the list by reporting two Myxomycetes which attacked fungous sporophores in Malaya. He observed the plasmodium of *Physarum viride* var. *rigidum* (*P. rigidum* G. Lister) attacking the fructifications of *Schizophyllum commune* and *Hirneola hispida* but not the fructifications of *Daldinia concentrica*, *Ustulina zonata*, and *Nummularia pithodes*. Likewise, he observed the dirty gray plasmodium of *Trichamphora pezizoides* covering and feeding upon the fruitbodies of *Schizophyllum commune*, "*Tremellina* sp.", *Daldinia* sp., and *Ustulina zonata*.

An examination of the foregoing résumé of the literature shows that of the seven mycophagous species of Myxomycetes reported, all belong to the family *Physaraceae* and that yellow-colored plasmodia predominate. Species classified in other families have been observed by the authors to be parasitic upon fungous tissues, to an account of which we now turn.

MYXOMYCETES FOUND TO BE PARASITIC AND THEIR FUNGUS HOSTS

During these investigations, thirty-three different plasmodia were tested for their parasitism upon fruitbodies of Hymenomycetes. Fifteen species, representing four families of the Myxomycetes, were identified as follows: *Badhamia foliicola* List., *B. magna* Pk., *B. rubiginosa* Rost., *B. utricularis* Berk., *Fuligo septica* Gmel., *Physarum flavicomum* Berk., *P. polycephalum* Schw., *P. tenerum* Rex., *P. virescens* Ditm., *Leocarpus fragilis* Rost., *Brefeldia maxima* Rost., *Lindbladia effusa* Rost., *Lycogala epidendrum* Fr., *Hemitrichia clarata* Rost., and *Trichia decipiens* Macbr. Of the eighteen remaining plasmodia used, one was found to belong to the genus *Lamproderma* and another to the genus *Physarum*, but the others either failed to form sporangia or the sporangia were so aberrant that they could not be identified. These unidentified plasmodia were white, gray, yellow, and red in color, and were proved to be but weakly parasitic with one exception, plasmodium BFU, whose host range will be given later. Notes on the parasitism of the

various identified species, as exhibited in the forest and by laboratory tests, are presented in the following paragraphs.

Badhamia foliicola List. was found creeping over and feeding upon many fruit-bodies of *Polyporus resinosus* by A. W. McCallum in the late autumn of 1918. The bright yellow plasmodium was eroding and channeling the pore surface noticeably.

Badhamia magna Pk. seems to be selectively parasitic, since the plasmodium grew rapidly at the expense of the tissues of *Collybia succosa* and *Trametes pini*, slightly increased in size but did little damage to *Fomes applanatus*, and died upon sporophores of *Collybia hygrophoroides*, *Coprinus micaceus*, and *Mycena galericulata*.

Badhamia rubiginosa Rost. increased slightly in size upon *Collybia hygrophoroides*, *C. succosa*, and *Polyporus versicolor*, but failed to attack *Amanita flavoconia*, *Coprinus micaceus*, *Cortinarius lilacinus*, *Hypholoma sublateritium*, *Mycena galericulata*, *Pleurotus ostreatus*, *P. sapidus*, *Polyporus betulinus*, and *P. sulphureus*.

Badhamia utricularis Berk. apparently may frequently attack *Polyporus resinosus* in the forest, since four collections of eroded sporophores of this fungus bearing *Badhamia utricularis* sporangia are represented in the University of Toronto herbarium. One very large sporophore of *Polyporus resinosus*, consisting of several subimbricate laterally connate brackets, the largest 16 cm. wide and the smallest 8 cm. wide was collected by Professor Faull. Practically the whole of the pore surface was demolished and the upper surface was furrowed where all of the fluffy superficial tissues had been consumed.

Physarum flavicomum Berk. was found attacking a fresh fruit-body of *Lentinus lepideus* in the field in October 1919 by J. H. Faull. The greenish-yellow plasmodium had reduced the gills to a slimy bacteria-infested mass. Later the same species was found on one occasion attacking the pore surface of *Polyporus lacteus* and on another, rapidly destroying a large group of *Merulius tremellosus* sporophores. These plasmodia were brought into the laboratory, kept in culture upon agar media, and used to inoculate other species of mushrooms. Although the plasmodium is a gross feeder it does not attack all of the fungi with equal intensity, so, for convenience, the fungi are grouped according to the character of the attack by the Myxomycete. Included in the group of Hymenomycetes upon which the plasmodium flourished especially, so that it rapidly increased in size and more or less eroded the whole fruitbody before moving away, are: *Flammula polychroa*, *Lentinus*

leptideus, *Merulius tremellosus*, *Pleurotus ostreatus*, *P. serotinus* (Plate 49, fig. 9), and *Polyporus resinosis*. In the group upon which the plasmodium became so sluggish that it rarely moved away before both the sporophore and itself were attacked by secondary invaders are: *Collybia velutipes*, *Hypholoma sublateralitum*, *Mycena* sp., *Pholiota marginata*, *Psalliota campestris*, *Polyporus adustus*, and *P. pargamensis*. A third group, *Armillaria mellea*, *Claudopus nidulans*, *Clitocybe multiceps*, and *Pleurotus ulmarius* were only slightly attacked by the plasmodium which usually died before it caused much damage. The last group includes those sporophores which the plasmodium failed to attack, namely; *Gyrocephalum* sp., *Lycoperdon* sp., *Tremella* sp., and *Tricholoma personatum*.

Physarum polycephalum Schw. plasmodia are quite frequently found destroying mushrooms and Polypores in the woods. Sporangia were collected in the summer of 1917 by J. H. Faull at Alexandria, Pa., and at Ithaca, New York, where before forming spores the plasmodia had been feeding on *Pleurotus ostreatus*. In July 1921 a large maple log was discovered bearing hundreds of *Pleurotus ostreatus* sporophores most of which were reduced to slimy pendant masses by the yellow plasmodium of *Physarum polycephalum*. Intermixed with the *Pleurotus* fruitbodies were fresh sporophores of *Fomes applanatus* and nearby was a cluster of *Mycena Leaiana* which were untouched by the plasmodium. Ten days later, on another maple log fifty yards from the one upon which the former collection was made, a large number of sporophores of *Pleurotus petaloides* was found scarcely one of which was not attacked by *Physarum polycephalum*. Again in early September of the same year a dead Elm tree was discovered with clusters of *Pleurotus ostreatus* intermixed with *Fomes applanatus* at its base, and while the former were being consumed by the plasmodium of *Physarum polycephalum*, the latter were untouched. One of the sporophores of *Fomes applanatus* was brought into the laboratory and there inoculated with a plasmodium which rapidly attacked the hymenium, as shown in plate 49, fig. 10.

The results of inoculations of fungous fruitbodies show that with *Physarum polycephalum*, as is also true for the other species investigated, the plasmodium does not attack all fungi with equal intensity. Some plasmodia may attack only the hymenial surface or the trama of a pileus while others may destroy the entire sporophore, none will wholly consume any fruitbody—there is always an undigested residue even though it be but the merest outline.

The fungi inoculated with the plasmodium of *Physarum poly-*

cephalum are grouped according to the ability of the Myxomycete to parasitise them. Those on which the plasmodium increased rapidly in size by digesting a large part of the sporophore are: *Amanita flaroconia*, *A. muscaria*, *A. phalloides*, *A. verna*, *Amanitopsis raginata*, *Armillaria mellea*, *Cantharellus cibarius*, *Claudopus* sp., *Clitocybe dealbata*, *C. illudens*, *C. multiceps*, *Clitopilus prunulus*, *Collybia dryophila*, *C. radicata*, *Coprinus atramentarius*, *C. micaceus*, *Cortinarius lilacinus*, *Hygrophorus Peckianus*, *Hypholoma sub*



Fig. 1. A. Sporophores of *Mycena alcalina* inoculated twelve hours previously with the plasmodium of *Physarum polycephalum*. Several fruitbodies on the left have been enveloped by the plasmodium and have collapsed on the substratum. B. Twenty-four hours later practically every sporophore has been attacked and many have been left as soft black masses of tissue.

lateritium, *Lactarius volemus*, *Lepiota brunnea*, *L. naucina*, *Mycena haematopa*, *Pleurotus petaloides*, *P. serotinus*, *P. ostreatus*, *Pluteus cervinus*, *Russula roseipes*, *Tricholoma album*, *Boletus scaber*, *B. speciosus*, *Merulius tremellosus*, and *Polyporus betulinus*. It seems

strange that *Polyporus betulinus*, although much firmer in texture than other members of the above group, is hardly surpassed as a host for *Physarum polycephalum*.

The fungi which were attacked more slowly, but on which the plasmodium fed for a comparatively long time, are: *Fomes applanatus* (Plate 49, fig. 10), *Lenzites betulina*, *Polyporus adustus*, *P. fron-*



Fig. 2. A. Sporophores of *Boletus subtomentosus* twelve hours after inoculation with *Physarum polycephalum*, showing the plasmodium eroding the stipe and destroying the adjacent pores of the fruitbody on the left, and moving over the stipe of the one on the right. B. Twenty-four hours later the pileus at the left is a soft disintegrating black mass. The pores of the pileus on the right are about to be attacked.

dosus, *P. hirsutus*, *P. pargamenus*, *P. resinosus*, *P. Schweinitzii* (Plate 48, figs. 3-4), and *P. versicolor*. The sporophores which *Physarum polycephalum* attacked virulently, but oftentimes from which the plasmodium moved so sluggishly that when putrefaction

began it disintegrated with the host, are: *Collybia succosa* (Plate 48, figs. 1-2), *Flammula polychroa*, *Hypholoma appendiculatum*, *H. velutinum*, *Mycena alcalina* (Text-fig. 1), *Pholiota praecox*, *Pleurotus sapidus*, *Psalliota campestris*, *P. placomyces*, *P. Rodmani*, *Russula fragilis*, *Boletus felleus*, *B. subtomentosus* (Text-fig. 2), *Strobilomyces strobilaceus*, *Polyporus sulphureus*, *Hymenochaete badio-ferruginea*, *Hydnum repandum*, *H. septentrionale*, *Hydnelium scrobiculatum*, *Clavaria aurea*, *C. fusiformis*, *C. Kunzei*, and *Tremella lutescens*. The plasmodium of *Physarum polycephalum* failed to attack *Claudopus* sp., *Clitocybe pithyophila*, *Pleurotus ulmarius*, *Tricholoma personatum*, *Poria corticola*, and *Lycoperdon* sp.

Positive statements regarding the intensity of the plasmodial attack upon a certain fungus host are difficult to make, since the maturity and condition of each sporophore tested may make a difference. In some trials *Hydnum septentrionale* was not attacked after inoculation with the plasmodium of *Physarum polycephalum*, while in other trials the plasmodium consumed almost the entire sporophore. The same was true of *Amanita phalloides* and of *Russula emetica*. A good example of the effect of the maturity of the sporophore upon the parasitism of the Myxomycete was shown by *Physarum polycephalum* upon *Coprinus micaceus*. If the plasmodium was placed upon the gills of a young pileus, the plasmodium grew rapidly at the expense of the gills and trama, but if the gills had changed in color from white to reddish purple or had begun to deliquesce, the plasmodium was killed.

Physarum tenerum Rex. rapidly attacked *Merulius tremellosus*, but very slowly attacked *Coprinus atramentarius*, *Lepiota brunnea*, *Polyporus adustus* and *P. pargamenus*.

Physarum virescens Ditm. was unable to attack *Coprinus micaceus*, but made a slight growth upon *Collybia succosa*.

Fuligo septica Gmel. failed to attack the sporophores of *Clitocybe multiceps* and *Clitopilus prunulus* when the typical yellow plasmodium was used as inoculum. When two white plasmodia, whose aethalia formed in cultures have been identified as *Fuligo septica*, were tested on fungi, they destroyed the tissues of some fruitbodies. The sporophores of *Amanita muscaria*, *Pleurotus petaloides*, *Tricholoma album*, *Boletus scaber* and *Merulius tremellosus* were rather rapidly attacked, while those of *Amanita phalloides*, *A. verna*, *Lactarius volemus*, *Lepiota naucina*, *Pleurotus ostreatus*, *Boletus speciosus*, *Polyporus Schweinitzii*, and *Tremella lutescens* were attacked more slowly. The fruitbodies of the following fungi were not attacked: *Hygrophorus Peckianus*, *Russula emetica*,

Polyporus betulinus, *P. sulphureus*, *Poria corticola*, and *Hydnum septentrionale*.

Leocarpus fragilis Rost. increased slightly in size upon sporophores of *Collybia succosa*, but fruitbodies of *Coprinus micaceus*, *Mycena galericulata*, *Fomes applanatus*, and *Trametes pini* inoculated with the plasmodium were unattacked.

Brefeldia maxima Rost. made a slight growth upon *Collybia hygrophoroides* and *Fomes applanatus*, but none on the pilei of *Coprinus micaceus*.

Lindbladia effusa Rost. failed to grow on *Mycena galericulata* and *Coprinus micaceus*.

Lycogala epidendrum Fr. made a slight growth upon the apothecium of a *Peziza* and upon the mushroom *Mycena galericulata*, but it failed to attack *Mycena Leaiana* and *Coprinus micaceus*.

Hemitrichia clavata Rost.; the plasmodium attacked sporophores of *Mycena galericulata* and made a fair growth upon them, but it failed to attack *Collybia hygrophoroides*, *C. succosa*, *Coprinus micaceus*, and *Mycena Leaiana*.

Trichia decipiens Macbr. grew quite rapidly at the expense of the tissues of *Mycena Leaiana*, grew slightly upon *Mycena galericulata* and *Collybia hygrophoroides*, but did not attack *Coprinus micaceus*.

Lamproderma sp. seemed to attack *Hypholoma sublateritium* slowly but proved innocuous on *Pleurotus ostreatus*, *P. petaloides*, *P. sapidus*, *P. ulmarius*, and *Poria corticola*.

An unidentified yellow plasmodium (BFU) proved to be extremely parasitic and rapidly destroyed *Coprinus atramentarius*, *Hypholoma sublateritium*, *Lepiota brunnea*, *Pleurotus ostreatus*, *Russula emetica*, *Boletus scaber*, *Merulius tremellosus*, *Polyporus betulinus*, *P. adustus*, *Poria corticola*, *Daedalea confragosa*, and *Hymenochaete badio-ferruginea*.

The number of Myxomycetes whose plasmodia utilize fungi for food is far from being known and must await the cumulative observations of more workers in the future. Likewise, the complete range of fungi one species of plasmodium may parasitize is not known, but we may safely conclude from the long list of fungi that *Badhamia utricularis* and *Physarum polycephalum* are known to attack, that some species are very general parasites. Other species, as yet, appear to be non-parasitic upon fungi.

The tougher, more resistant tissues of the woody Polypores

account for the slower attack by plasmodia upon them. The plasmodia move over the surface of the pores digesting the basidial layer and sometimes completely destroying the pores, as seen in Plate 48, figs. 3-4. As a contributing factor of great importance in the destruction of the sporophores, it should be noted that all the observed plasmodia remove the surface layers and leave the Polypore with a moist slimy coating; a very favorable substratum for the development of Mucors, bacteria, and other secondary invaders.

This parasitism of Myxomycetes on fructifications of fungi is not confined to the laboratory, for during one season (1931) twenty-two plasmodia were found in the forest apparently feeding on the fungi with which they were associated. Birch and maple logs, decayed by various Polypores and Agarics, proved to be a favored haunt of the majority of these plasmodia, but three were found destroying fungi on an oak stump, one on a dead standing Chestnut (*Castanea dentata*), and another on a dead standing Pine. Although field observation of the parasitic habit of plasmodia first aroused our interest in this problem, study in the laboratory has given us some details of the method of attack.

DISCUSSION OF THE METHOD OF ATTACK

Microscopical examination of both living and sectioned material shows that the attack of plasmodia upon all of the sporophores examined to be both pathogenic and parasitic; pathogenic in that the plasmodium may cause necrosis of the living fungous tissues with which it comes in contact, and parasitic in that the fungous tissues are digested and then absorbed to furnish nutrients for the growth and activities of the plasmodium.

Pinoy (10) doubts that plasmodia have the power of digesting fungous mycelium. He believes that the breakdown of the fungous tissues is due to associated bacteria and to the water absorbing power of the plasmodium which is supposedly able to dry up and kill the mycelial filaments without digesting them. Some of the evidence found by the authors to oppose this view is: 1, living hyphae with no signs of bacteria surrounding them can actually be seen to dissolve throughout their length when covered by the plasmodium, 2, stained sections (Plate 48, figs. 6-7) have failed to reveal bacteria digesting the hymenial layer in order that the plasmodium might absorb the by-products, 3, a normally non-parasitic plasmodium after being allowed to move over a culture of bacteria or of yeasts, which have been found associated with an actively parasitic plasmodium, does not become mycophagous when given the opportunity to digest fungous material.

The process of destruction appears to be of a chemical nature, as is evidenced by observing the individual hyphae in contact with the plasmodium gradually lose their sharp outlines and become dissolved. The time required for the dissolution of the fungous tissue seems to vary with the digestive secretions of the plasmodium, but no special study of this digestive process was made. The nature of the hyphal wall appears to play an important role in susceptibility to plasmodial attack, as is shown by their attack on hyaline hyphae more readily than on colored ones. No microchemical tests of the hyphal walls have been made with which this specificity could be correlated. The thickness of the fungous wall likewise appears to be directly proportional to the length of time necessary for its digestion by the plasmodium, as is shown by thin-walled hyaline hyphae of the hymenium actually dissolving away within a few seconds after coming in contact with the advancing margin of the plasmodium, while thick-walled hyphae either may require several minutes for their dissolution and may be found several millimeters behind the advancing margin before they break down, or they are not digested but are left as debris.

In order to dispel any possible idea that digestion occurs in advance of the plasmodium, it is emphasized that the tissues to be digested must lie in close contact with the plasmodium. This contact, however, may be either with the surface membrane or with a vacuolar membrane. Although digestion of hyphae in vacuoles is a possibility, it could not be definitely demonstrated in stained preparations of plasmodia parasitising sporophores, but the hyphal tissues appeared to be digested without engulfment at the ventral surface of the plasmodium (Plate 48, fig. 5).

On the other hand spores appear to be more generally enclosed in vacuoles for digestion. An excellent example of the ingestion of spores was witnessed when sections of the plasmodium of *Physarum polycephalum* attacking the lamellae of *Hypholoma sublateralitium* were examined (Plate 48, figs. 6-7). The smooth, oblong-elliptical, purple-brown spores, measuring 3-4 x 6-7 microns, may be clearly seen enclosed in vacuoles in the matrix of the plasmodium. In Plate 48, figs. 6-7, the spores are shown near the ventral surface of the plasmodium and the nuclei near the dorsal surface. The plasmodium is highly vacuolate in its ventral portion where it is assimilating nutrients. Very large, dark-colored, thick-walled spores are many times not ingested but merely pushed aside mechanically by the plasmodium.

Although Lister (8) and others report that fungous tissues, spores, and other solid ingesta are engulfed and move in the pro-

toplasmic currents of the plasmodium, the authors have found that the plasmodium feeding upon a sporophore carries on practically all of its digestion of hyphae and spores close to the advancing margin. Only occasionally what appears to be a bit of hypha or a spore may be seen coursing through the plasmodial strands back of the advancing edge.

A study of sections of the pileus of *Pleurotus serotinus* attacked by the plasmodium of *Physarum flavicomum* shows the gills becoming more and more eroded until there remains only a small shapeless mass of indigestible residue. In Plate 48, fig. 5 the basidial layer has completely disappeared and the tissues underneath the plasmodium are being dissolved. There is a sharp line of demarcation between the plasmodium and the fungus. As soon as the basidial layer is dissolved on one gill, the *Myxomycete* moves to that of the next.

SUMMARY

Attention is called to the ability of plasmodia of *Myxomycetes* to parasitise the fruitbodies of common wood-rotting fungi. Some species of *Myxomycetes* have been shown by field observations and laboratory tests to be very generally parasitic upon *Hymenomycetes*, while other species are moderately so, or as yet, non-parasitic. In the laboratory about eighty-five species of the *Hymeniales*, ranging from fragile fleshy *Agarics* to hard woody *Polypores*, were inoculated and most of them were found to be attacked by one or more of the thirty-three different plasmodia used in this study.

Plasmodia of the following species are now known to be mycophagous: *Badhamia foliicola*, *B. magna*, *B. rubiginosa*, *B. utricularis*, *Brefeldia maxima*, *Fuligo septica*, *Hemitrichia clavata*, *Leocarpus fragilis*, *Lycogala epidendrum*, *Physarum flavicomum*, *P. polycephalum*, *P. rigidum*, *P. tenerum*, *P. virescens*, and *Trichia decipiens*. Many other plasmodia, as yet unidentified, exhibited various degrees of parasitism. Unaccounted for preference for some fruitbodies is exhibited by the plasmodia. Mushrooms poisonous to man are readily parasitized by plasmodia, but the maturity of the sporophore does affect the parasitism of the *Myxomycete*.

The plasmodia bring about the destruction of the sporophores in two ways: 1, by actively digesting the sporophores themselves, and 2, by leaving the moist, slimy, injured fungous tissues, over which they have passed in an ideal condition for infection by bacteria and fungi which carry the destruction further.

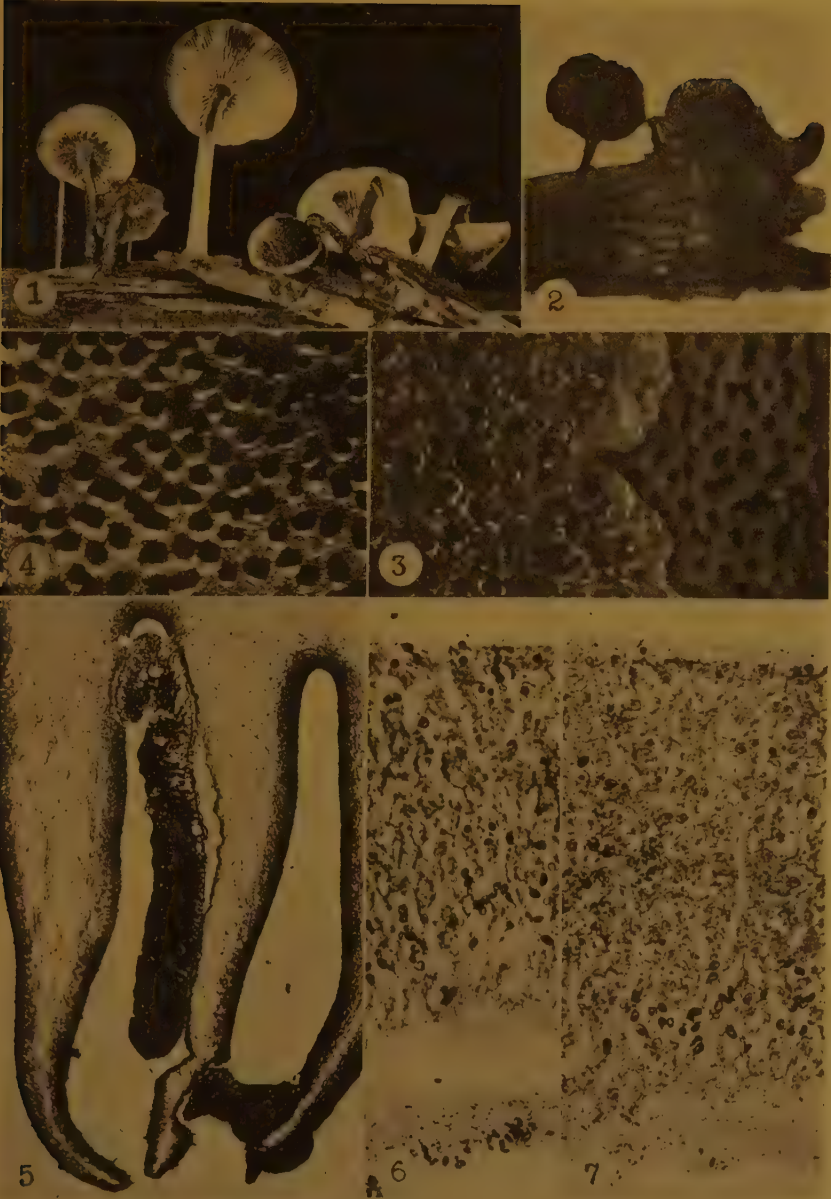
The process of destruction of the sporophores is one of digestion, the basidial layer being usually the first tissue attacked. Hyphal tissues are digested at the highly vacuolate ventral surface of the plasmodium without enclosure within the vacuoles, while the spores are usually ingested and then digested within the vacuoles.

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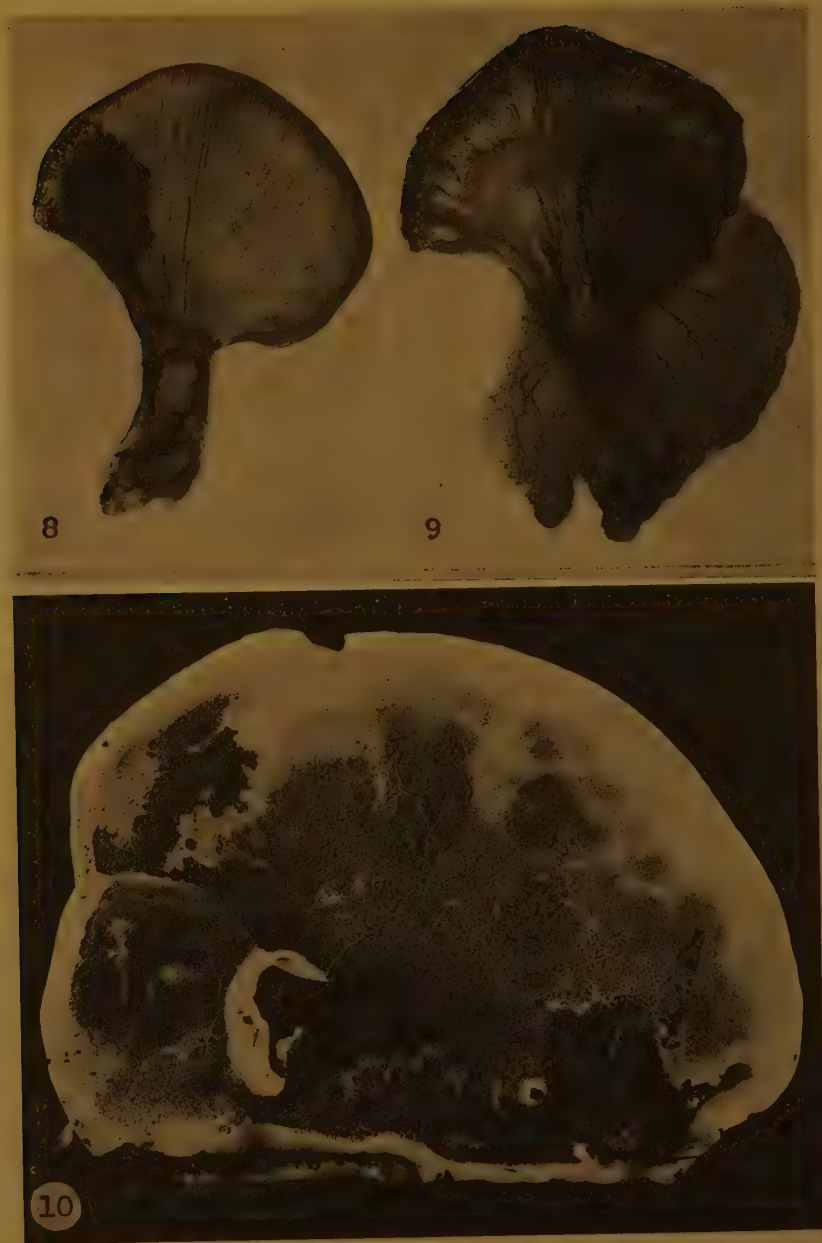
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EXPLANATION OF PLATES 48 AND 49

- Fig. 1. Fruitbodies of *Collybia succosa* which had been inoculated with *Physarum polycephalum* twelve hours previously. The two sporophores on the left are held erect with pins due to destruction of their stipes by the plasmodium.
- Fig. 2. Twenty-four hours later the plasmodium has reduced all of the fruitbodies to moist blue-black masses of tissue.
- Fig. 3. Pore surface of *Polyporus Schweinitzii* being attacked by the plasmodium of *Physarum polycephalum*. $\times 8$.
- Fig. 4. The same pore surface after the plasmodium has passed over it. Note the thin pore walls left behind. $\times 8$.
- Fig. 5. Photomicrograph of gills of *Pleurotus serotinus* being attacked by the plasmodium of *Physarum flavicomum*, showing the manner in which the tissues are digested. Observe the sharp line of demarcation between the darkly stained plasmodium and the tramal tissue. Section cut 10μ thick and stained with Flemming's triple. $\times 63$.
- Fig. 6. Photomicrograph of the plasmodium of *Physarum polycephalum* shown digesting the hymenium and ingesting the spores from a gill of *Hypholoma sublateritium*. The trama and hymenial layer on one side of the gill has been digested but the hymenial layer on the other side of the gill is shown at the bottom of the picture. $\times 295$.
- Fig. 7. Photomicrograph of another portion of the plasmodium and gill shown in Fig. 6. Here is shown a bit of the trama at the bottom of the section, the dark colored spores ingested in the vacuolate ventral portion of the plasmodium, and the stained nuclei with their nucleoli which appear as bulls-eyes in the dorsal portion of the plasmodium. Paraffin section cut 3μ thick and stained with iron-alum-haematoxylin. $\times 295$.
- Fig. 8. *Pleurotus serotinus* inoculated with the plasmodium of *Physarum flavicomum*.
- Fig. 9. Twenty-four hours later the plasmodium has destroyed the gills, leaving behind a moist, slimy surface ideal for the growth of bacteria and saprophytic fungi.
- Fig. 10. A sporophore of *Fomes applanatus* twenty-four hours after being inoculated with the yellow plasmodium of *Physarum polycephalum*. The fluffy white surface layer of hyphae is being removed thus allowing the eroded brown pore surface to show through.



PARASITISM OF PLASMODIA ON SPOROPHORES



PARASITISM OF PLASMODIA ON SPOROPHORES

STUDIES ON THE PRECIPITIN REACTION IN PLANTS

II. PRELIMINARY REPORT ON THE NATURE OF THE
"NORMAL PRECIPITIN REACTION"

KENNETH S. CHESTER

IN 1928 Kostoff first called attention to the fact that the aqueous extracts of the foliage of certain Solanaceous plants precipitate in the presence of certain other such Solanaceous extracts (3). This precipitating action was designated as a "normal precipitin reaction," and the modification of such reactions after intergrafting underlies in part Kostoff's theory regarding acquired antibody production in such plants. In 1931 the writer published a record of his tests of the "normal precipitin reactions" in a number of species of the Oleaceae (1). These tests showed that the species of Oleaceae tested were in no case interreactive with the exception of numerous varieties of *Syringa vulgaris* which were suffering from a physiological blight due to graft incompatibility. Such varieties reacted strongly against a number of other Oleaceae including healthy, ungrafted plants of the same varieties as the reactive plants. Meanwhile Silberschmidt in Munich had also been studying the Kostoff phenomenon from the standpoint of technique. Silberschmidt has published an extended piece of research dealing mainly with improvements of the methods of extracting and testing (4), and he intended, at the time of publication, a continuation of his work dealing with the actual experimental results of his tests. Early in 1932 there appeared a second paper by the writer (2) showing that the "normal precipitin reactions" between species of the Rosaceae, Saxifragaceae, and Caprifoliaceae are well correlated with the systematic positions of the species considered.

Thus far little attempt had been made to determine the biochemical nature of the reaction. Kostoff and Silberschmidt both assume that the phenomena are of protein nature, and that they are analogous to the phenomena of animal serology. In 1932, however, the writer stated that: "Some of the reactions, such as those of *Prunus*, *Ribes*, and *Robinia*, lead one to the suspicion that possibly some non-specific compound is acting in a rather complex fashion to produce the precipitates" (2, page 71). The problem of the chemical nature of the "precipitin reaction" thus lay open to investigation and was of utmost importance in interpreting and evaluating the results of the earlier experiments. In the phytopathological laboratories of the Arnold Arboretum investigations have accordingly been in progress during the past

winter to determine the chemical nature of the precipitating property of the extracts. As these investigations have been fruitful and as the results are of importance in directing future activities in this field, the present paper is designed to give a condensed account of these results, while a more detailed description of the work will appear in an early number of this Journal.

In the fall of 1931 collections of leaves of certain species of woody plants were dried and pulverized. These relatively homogeneous stock supplies were used for all the tests of woody plants described below. The technique employed was in all important particulars the same as that previously described (2). Among the species selected were *Prunus Armeniaca* var. "Mikado," *Platanus acerifolia*, *Robinia fertilis*, and \times *Ribes Carrierei*. Of these four the *Prunus* tests strongly against the other three which latter are mutually inter-negative. The results obtained from a study of these four species were later found to apply to extracts of *Hydrangea paniculata* var. *grandiflora*, *Syringa vulgaris*, *Ligustrum obtusifolium*, *L. ibota*, and *L. vulgare* var. *foliosum*. Finally, the findings were applied to thirty-five species of Solanaceae, and accordingly the results here recounted have been gained from a study of practically all of the possible inter-reactions of forty-four species of herbaceous and woody plants.

As a working hypothesis the theory was first entertained that the reactions might be of protein nature. Accordingly the earlier part of the investigation dealt with an analysis of the reactions on the basis of such an hypothesis. However, the results obtained from an analysis of the *Prunus-Robinia-Platanus-Ribes* reactions showed a very peculiar behavior if such an hypothesis were correct. The findings in this connection are here enumerated:

1. Variation in the salt content of the extracts by the use of Cohn's phosphate buffers at constant pH of 6.0 had very little effect on the reactive potency of *Prunus* between the limits of .06 M and 1.2 M. Between the same limits, however, there was a gradual fall in reactive potency of *Platanus* and *Robinia* from the weaker to the stronger salt concentrations.
2. Variation of the pH of the extracts by the use of Cohn's phosphate buffers at constant salt concentration of .06 M had no effect on *Robinia* between the limits of 5.2 and 8.4, and also no effect on *Prunus* between the same limits except for a sharp decline from 8.0 to 8.4 and from 5.6 to 5.2.
3. Long continued heating (even to three hours autoclaving at 5 lbs. pressure) did not decrease the reactive strength of either *Prunus* or *Robinia* extracts.

4. Precipitation of the extracts of *Prunus* or *Robinia* by excessive alkalinity or acidity, followed by filtration and subsequent neutralization did not remove the reactive principles.
5. There was no significant effect on the strength of the reaction if the pulverized leaves were thoroughly extracted with strong alcohol, anhydrous ether, benzol, or carbon tetrachloride as a preliminary to extraction with water.
6. There was no diminution in reactivity after storing the extracts at 2° C. for as much as four months. Even bacterial or fungous contamination had little or no effect on the strength or specificity of the reaction, when the extracts were subsequently cleared.
7. The progressive dilution of each of the extracts in turn showed an almost linear diminution in reactivity, the reaction disappearing in *Platanus* between dilutions of 1 : 256 and 1 : 512 and in *Prunus* between dilutions of 1 : 64 and 1 : 128. (Note: Normality of the extracts was arbitrarily chosen at 1 part dried tissue to 10 parts distilled water. The dilutions referred to here were further dilutions of such normal extracts.)
8. The reactivity of the extracts was unaffected by continued digestion with trypsin, pepsin, and yeast enzymes at appropriate pH values and temperatures.
9. Complete precipitation of *Prunus* by *Robinia*, *Platanus*, *Ribes*, or *Hydrangea* completely eliminated any further reaction of the thus-precipitated *Prunus* by any other of the latter four.
10. Fractionation of the extracts by the Rimington technique for removing carbohydrates showed that the reactive principle of *Prunus* was precipitated by neutral lead acetate and was entirely recoverable from that precipitate on treatment with H₂S. The reactive principles in *Robinia* and *Platanus*, on the other hand, were unaffected by treatment with both neutral and alkaline lead acetate and were completely recoverable in the nearly Molisch-negative filtrate from such treatment.
11. Extensive dialysis experiments showed that the reactive principles of *Prunus*, *Platanus*, and *Robinia* passed freely through membranes impermeable to formed proteins and only very slightly permeable to protein cleavage products. The strength of the reactive principles thus fractionated varied directly with the strength of chloride and carbohydrate (used as indices of the degree of dialysis) and bore no relation whatever to the strength of protein as indicated by the Millon and xanthoproteic tests (used as indices of the degree of dialysis).

Reviewing the evidence presented, the probability that the *Prunus-Platanus-Robinia-Ribes* reactions are due to proteins is

very slight. Although plant proteins are more resistant to heat than animal proteins and accordingly the results in heating the extracts are inconclusive by themselves, yet it is inconceivable that proteins would not be removed or inactivated by treatment with acids and alkalis and with alcohol, by salt content and pH, by contaminations and enzyme action, and by the removal of various constituents of the extracts as must be the case if proteins are here involved. The identity of the various reactions of these species (item 9 above) argues against the protein hypothesis, and finally the experiments in dialysis show that it is extremely unlikely that the reactions are due to extremely small traces of protein. The likelihood that these reactions are due to lipoids or to carbohydrates is also very dubious in view of the results given in items 5 and 10 respectively.

In the course of an experiment on hydrolysis of the extracts a small excess of CaCO_3 was added to a sulphuric acid solution of *Prunus*. On neutralization it was found that its precipitating action was completely reversed. The presence of the calcium sulphate thus formed, although only very slightly soluble in water, rendered the *Prunus* negative to *Platanus*, *Robinia*, and *Ribes*, and, as was later found out, positive to extracts with which it had formerly been negative. Attention was accordingly directed to the inorganic constituents of these extracts with particular reference to calcium compounds.

This last was a most productive field. It was soon discovered and confirmed that the reactions in the woody plants under consideration are due to the interaction of free calcium ion in certain extracts (in this case in *Robinia*, *Platanus*, and *Ribes*) with free oxalate ion in the other extracts (represented for the present by *Prunus*). Such a view has resulted both from chemical analyses of the precipitates and from studies of the behavior of the whole extracts with regard to presence or absence of calcium and oxalate. The analytical evidence supporting the view that these reactions are due to the interaction of such ions in first presented:

1. The precipitates, after washing in several changes of water, are white, heavy, limey, easily centrifuged, and inorganic in appearance. There is no charring on heating to 500°C .
2. The precipitates microscopically are in the form of regular granules, not amorphous, identical in appearance with certain commercial samples of calcium oxalate.
3. Recrystallization of the precipitates (by solution in strong H_2SO_4 and precipitation by neutralization with strong KOH) gives crystals of the characteristic size and shape of CaC_2O_4 .

crystals, and indistinguishable from crystals of a commercial sample of CaC_2O_4 similarly treated.

4. Treatment of the granules of the precipitates with strong H_2SO_4 under the microscope shows first a moderate solution followed by a very striking conversion of the remainder of the granules into the characteristic raphides of CaSO_4 . This is a fairly accurate test for CaC_2O_4 and is precisely the behavior of a sample of commercial CaC_2O_4 similarly treated.
5. The precipitates are insoluble in all ordinary solvents. They are moderately soluble in strong H_2SO_2 but not in weaker acids. Their solubilities are thus equivalent to those of CaC_2O_4 .
6. If alcohol is added to the H_2SO_4 solution of the precipitates there is a precipitation. (Test for calcium ion.)
7. The acid solution reduces potassium permanganate. (Test for oxalates).
8. Ignition of the washed precipitate yields 33% of oxide. The theoretical yield for CaC_2O_4 is 38%.

The evidence thus given leaves no room for doubt that the precipitates resulting from the addition of the *Prunus* extract to those of *Platanus*, *Robinia*, and *Ribes* consist of calcium oxalate. This evidence is still further confirmed by experiments to be reported below. At this time, however, certain questions arise: (a) Is this calcium oxalate reaction the only one involved in the combinations of woody plants under consideration? (b) How generally is the calcium oxalate reaction distributed through plants with especial reference to the tests which have been reported in the literature? (c) Are other reactions also involved in the tests which have been reported, and if so, what is their nature? The answers to these questions will appear from the following considerations.

If the calcium oxalate reaction is the main or only reaction in the woody plants available for this study it should be possible to divide all the extracts into two groups, a calcium-positive, oxalate-negative group which is intranegative but positive to a second, oxalate-positive, calcium-negative group. Such is possible. *Prunus Armeniaca* "Mikado" is here the only representative of the "oxalate" group (containing oxalate, lacking calcium), while the "calcium" group comprises *Platanus*, *Ribes*, *Robinia*, *Syringa*, *Hydrangea*, and the three species of *Ligustrum*. With the exception of a very weak reaction to be mentioned later, the latter group is perfectly intranegative. On the other hand, the members of this "calcium" group all produce precipitates identical in appearance with the "precipitin reaction" when they are added to weak solutions of

oxalates ($K_2C_2O_4$.01 M; $(NH_4)_2C_2O_4$.02 M) but are inactive to the addition of weak solutions of calcium salts ($CaCl_2$.005 M; $Ca(NO_3)_2$.005 M). *Prunus*, however, reacts positively to pure solutions of calcium salts of the concentrations given above but is negative to these oxalates.

At this juncture it was felt advisable to extend these results to the Solanaceae for the dual purpose of obtaining more extensive data, and of obtaining data on the family on which the work of Kostoff and Silberschmidt has been done. Accordingly, all the possible interreactions of thirty-five species of Solanaceae as well as all their reactions with the woody plants under consideration were carried out by the writer in collaboration with Dr. Thomas Whitaker. The results of these tests were highly confirmatory. Testing the various Solanaceae against weak solutions of two oxalates and of two calcium salts it was found that the species fell into three groups, a group (Ca- Ox+) comprising *Atropa belladonna*, *Solanum tuberosum*, *Capsicum frutescens*, *Physalis peruviana*, *Salpiglossis sinuata*, *Datura ferox*, *D. metel*, and *D. innoxia* which were all positive in varying degree to the calcium salts and negative to the oxalates, a group (Ca- Ox-) comprising *Datura Wrightii*, *Cyphomandra betacea* and *Browallia viscosa* which were negative to both ions, and a group (Ca+ Ox-) comprising eighteen species of *Nicotiana*, *Petunia violacea*, *Lycopersicum cerasiforme*, *Solanum capsicastrum*, *S. melongena*, and *S. nigrum* which were negative to free calcium ion but positive to free oxalate ion. The extracts of group (Ca- Ox+) were positive to those in group (Ca+ Ox-) but those of group (Ca- Ox-) were negative to all in both other groups. Moreover the strength of the "precipitin reactions" bore a very close relation to the strength of the reactions of the corresponding extracts with the pure salt solutions. The (Ca- Ox+) group was perfectly negative *inter se* and the (Ca+ Ox-) group was also negative *inter se* except for a few weak reactions principally involving *Datura Wrightii* and *Nicotiana Rusbyi*. Thus a consideration of the Solanaceae affords very strong confirmatory evidence as to the validity of the calcium oxalate explanation.

A warning should be introduced at this point. The writer is well aware of the fluctuations of the salt content in plant juices and makes no contention that the values for the reactions are definite and always exactly reproducible. The readings will vary with the observer, with the technique, and with the environment and heredity of the plants investigated. However, that high developments of the content of such inorganic constituents are characteristic of certain species is evident from a consideration of

the literature. Moreover that the results here described are comparable is evident from the facts that the layerings and readings were all made by the same observer, that all the reactions described for any given species of plant in this study were made from one given extract, that the Solanaceae were all grown under uniform greenhouse conditions, and that all of the "precipitin" tests described were made within a few days of one other.

An important confirmation should now result from testing the "calcium" Solanaceous extracts against the woody "calcium" extracts. If the calcium oxalate explanation be correct and complete, then such reactions should all be negative. In order to extend the limits of this experiment still farther, all the "oxalate" extracts, woody and herbaceous, were treated with a slight excess of CaCl_2 and filtered. Hence the calcium oxalate reaction was completely eliminated from consideration. Then all the possible combinations of the 42 extracts were again tested. This experiment brought out a very important fact. There is a second reaction in which *Platanus*, *Robinia*, and *Ribes* show a varying degree of reactivity against all the Solanaceae. The reactions of *Platanus*, *Robinia*, and *Ribes* are so well correlated here that it is most probable that there is a single substance (A) present in these three extracts which reacts with a second substance (B) in the Solanaceae. *Prunus*, *Syringa*, *Ligustrum obtusifolium*, and *L. ibota* react against neither the (A+ B-) nor the (A- B+) groups and accordingly are assumed to contain neither reactive principle.

It is now possible to eliminate both the calcium oxalate and AB reactions from consideration by considering only the interreactions of the 39 oxalate-negative, A-negative extracts. If this group of interreactions be studied it is seen that the great majority are negative (87%). There are a few scattered weak reactions, however, principally involving *Nicotiana Rusbyi* and *Datura Wrightii*. Rearranging all the remaining extracts according to their strength of reaction against the similar *N. Rusbyi* and *D. Wrightii* we find again that the 39 extracts are divisible into three groups, a group (M+ N-) comprising *N. Rusbyi*, *D. Wrightii*, *Cyphomandra*, *Ligustrum ibota* (?), and *Prunus* (?) which are positive to a group (M- N+) containing the remainder of the species with the exception of *Browallia*, *Salpiglossis*, *Petunia*, *Syringa*, *Ligustrum vulgare*, and *Solanum nigrum* (M- N-) which are negative to both groups.

There still remain a very few weak reactions (2%) which may be interpreted as due to a substance (X) present in *Solanum capsicastrum*, *Atropa*, *Physalis*, *Datura innoxia*, and *D. metel*

which reacts with a substance (Y) present in the Oleaceae studied, in *Browallia*, and in *Nicotiana suaveolens*, but absent in the other remaining extracts

These four reactions, the first proven, the second and third assuredly present and distinct but of unknown nature, and the fourth more problematical, since it is very weak, explain all of the thousand or fifteen hundred reactions considered in this study. Of all the positive reactions at least 57% are due to the calcium oxalate combination, approximately 23% to the AB reaction, 17% to the MN reaction, and less than 3% to the XY reaction.

We are now in a position to return to the questions propounded above. First, with regard to the presence of any other reaction in the *Prunus-Platanus-Robinia-Ribes* complex, we may say definitely that there is no other "precipitin" reaction demonstrable by the technique employed than the calcium oxalate reaction. Removal of the calcium oxalate reaction leaves these four extracts perfectly internegative. Second, as to the distribution of the calcium oxalate reaction among the experimental plants heretofore studied it may be said with certainty that this reaction is of wide distribution, that it accounts for the majority of the reactions of the plants used by Kostoff, and that it must be eliminated before any immunological interpretation can be made of the data thus far published. Kostoff published a table of "normal precipitin reactions" in the Solanaceae which includes 56 positive reactions. 40 of these have been repeated in this laboratory. Of the 40 repetitions, in 7 cases there were no positive results, in 10 cases the reactions were due to the MN combination, and in 23 cases the reactions were due to calcium oxalate. Kostoff reported acquirement of "precipitin potency" in 12 instances. The normal reactions as repeated in this study show that of the 8 repetitions 3 reactions were due to calcium oxalate, 3 were due to the MN reaction, and in 2 cases no positive results were obtained. Kostoff found a decrease of "precipitin potency" in 4 cases. 3 of these have been repeated and in all 3 cases the normal reactions were found to be due to the MN combination.

Third, as regards the presence and nature of other reactions in the plants considered, it may be said with certainty that there is at least one other reaction present, probably two, and possibly three or more. The nature of these other reactions is being investigated. For the time being, it may merely be said that with regard to the AB and MN reactions they are indubitably organic in nature since the washed precipitates are strongly charred on ignition. The precipitates of these reactions are very different in

appearance from the calcium oxalate precipitate. They are brown in color, even after washing, are copious and flocculent, and easily pass into a non-filterable colloidal suspension in pure water.

As further proof of the presence of more than one reaction, instances may be mentioned in which given extracts may be precipitated thoroughly to remove the calcium oxalate factor. Such calcium oxalate free extracts have lost none of their potency for precipitating in the presence of the opposite principle of the AB or MN reactions.

A word should be inserted at this point regarding the expressions "calcium" extracts, "oxalate" extracts, etc., frequently used in the foregoing pages. Such expressions do not imply that certain plants are free from demonstrable oxalate or calcium respectively, since the extracts used reveal the *excess* of either ion after such autoprecipitation of CaC_2O_4 as may take place in preparing the extracts. It is very apparent, for example, that *Prunus Armeniaca* vars. "Mikado" and *ansu* fall into the "oxalate" class not because they lack calcium but because they contain more than sufficient oxalate to neutralize the calcium normally present in the leaves.

With regard to the interpretation of the writer's earlier experiments in the light of the present findings, two questions arise: (a) Is the reaction of graft-blighted Lilac toward healthy Oleaceae (1) susceptible to explanation according to the calcium oxalate interpretation? (b) What light do the present findings throw on the specificity of the reactions as found in the Rosaceae et al. (2)? Both of these questions are readily understood by the results of the present paper.

In the first place, normal Lilac, and indeed the other species of Oleaceae studied, are all "calcium" plants, i. e. their extracts contain an excess of Ca^{++} ion. During the actual dying of the leaves of blighted Lilac there is an accumulation of oxalic acid or an oxalate in the affected cells. That this is not generally distributed throughout the plant (as would be true of an immunological substance resulting from grafting) is shown by the fact that the extracts made from green areas of mottled green-and-yellow leaves (blighted) test just as do normal leaves of ungrafted plants. The accumulation of free oxalate in the blighted portions of the leaves is in harmony with the fact that such leaves when ground and mixed with water begin an autoprecipitation (of the calcium normally present in the leaf by the oxalate) which if permitted to be carried to the end results in an excess of unused oxalate which gives the reaction with the other Oleaceae previously described. Immediately after maceration of the leaves, however, both oxalate and calcium can be demonstrated in the extracts.

Regarding the second question, as to the specificity of the reactions thus far observed, light was thrown upon this phase of the work by a consideration of the distribution of free calcium ion, free oxalate ion, and the other reactive principles in these various species of plants studied. On purely *a priori* grounds it would not be unreasonable to expect that in general the distribution of such substances would show some agreement with the taxonomic relationships of the plants involved. Thus it is well known that the presence or absence of calcium oxalate crystals in plant cells is of taxonomic significance. How does this apply to the Solanaceae and woody plants here studied? A dendritic chart was made including all the possible combinations of reactive substances believed to be responsible for the reactions observed. Thus the chart would first include a trifurcation representing presence of free calcium or free oxalate or absence of both. Each subdivision could then be further trifurcated according to presence or absence of the A and B principles, etc. There would thus be 81 possible combinations of reactive principles represented. If the assumption of specificity be correct, there should be a definite tendency for related species to have related positions on such a chart. The actual placement of the various species in their proper positions on such a chart brought out the validity of this assumption in striking clearness. 18 species of *Nicotiana* had been studied. All contain free calcium but not free oxalate, all contain the principle B but lack the principle A, *N. Rusbyi* alone contains the principle M, the other 17 species all contain N, while all the species of *Nicotiana* save *N. suaveolens* lack both X and Y. The possibility of their being so constituted by chance is infinitesimal. Similarly the Oleaceae considered are closely allied in all containing Ca^{++} , all lacking principles A and B except *L. vulgare* which has only a trace of this, all lacking both X and Y, and separating only with regard to the presence or absence of M and N. *Robinia*, *Platanus*, and *Ribes*, in closely related families, all are found to lie in the same quarter of the dendritic system, being all positive for calcium and for principle A, they being the only representatives of the A principle in the whole scheme. So, too, the 4 species of *Datura* as well as those of *Solanum* are found to agree in three of the four reactive principles, separating on only one.

It is thus seen that the distribution of the reactive principles in the 42 species of plants here considered is in good accordance with the taxonomic positions of these species, which clearly explains the earlier findings, before the nature of the reactions had been investigated, with regard to the specificity exhibited by the reaction.

SUMMARY

1. The present paper gives a condensed account of the writer's investigations of the biochemical nature of the "normal precipitin reaction" in plants.
2. Extensive experiments in the testing of various physical and chemical treatments have yielded strong evidence against the hypothesis that the reaction in certain woody plants, viz. *Prunus Armeniaca*, *Platanus acerifolia*, *Robinia fertilis*, and *Ribes Carrierei*, is of protein nature.
3. Conclusive proof is given that the reaction resulting in approximately 57% of the precipitates observed in all the possible combinations of 42 species of Solanaceous and woody plants is the precipitation of calcium oxalate by the interaction of the respective ions in pairs of extracts. This precipitation of calcium oxalate is so frequently the sole or main phenomenon in the reactions hitherto considered immunological in nature as to invalidate immunological interpretations laid on such reactions in which the calcium oxalate factor is not eliminated.
4. The remaining reactions are susceptible to interpretation on the assumption of the presence or absence of three other pairs of reactive substances. The nature of these reactive pairs is relatively obscure at present, but it is being investigated. One such pair (AB) is particularly characterized by the reactions of oxalate-free *Robinia*, *Platanus*, and *Ribes* with the Solanaceae. This reaction accounts for about 23% of the positive precipitations. It is shown to be distinct from the calcium oxalate reaction. A second pair (MN) is represented by the reactions of oxalate-free and AB-free *Nicotiana Rusbyi* and *Datura Wrightii* with most of the other Solanaceae. It is plainly distinct from the calcium oxalate and AB reactions and accounts for about 17% of the precipitations. A very small residue of reactions (less than 3%) is finally explained by the assumption of a last pair of reactive substances XY, the reactions being represented by those of *Solanum capsicastrum*, *Atropa belladonna*, *Physalis peruviana*, *Datura innoxia*, and *D. metel* against certain Oleaceae.
5. The writer's earlier findings with regard to "precipitin reactions" of physiologically blighted Lilac and to the specificity of the "normal precipitin reaction" are readily interpreted on the basis of the findings of the present study.

Acknowledgement is due for the many suggestions and freedom of his laboratory given the writer by Dr. Ronald Ferry of the Har-

vard Medical School, and to Dr. Thomas Whitaker who coöperated in the testing of the Solanaceae. The writer is also indebted to Professor E. M. East for placing the Solanaceae at his disposal and to Professor J. H. Faull for numerous helpful suggestions.

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NOTES ON SOME CHINESE PLANTS

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Hydrangea Chungii Rehder in Jour. Arnold Arb. XII. 69 (1931).

In the original description of this species the collector's numbers of the type and paratype were unfortunately omitted. These data are supplied below as well as additional records seen by the author.

FUKIEN: Yenping, Fort No. 3800, alt. 230 m., August 21, 1924, *H. H. Chung*, no. 3043 (holotype at the Arnold Arboretum, 2 sheets, one from University of California; isotype seen at Kew and Amoy); Yenping, Buong-kang, alt. 200-1000 m., June 8, 1925, *H. H. Chung*, No. 3260 (paratype at the Arnold Arboretum, also seen at Amoy); Yenping, Buong-kang, *S. T. Dunn*, Fukien Expedition, 1905, Hongkong Herb. no. 2663, also is this species (seen at Kew and Hongkong) as well as *S. T. Dunn*, Hongkong Herb. No. 2678, without data (seen at Hongkong).

Another specimen collected in 1909 by Schindler in "Südwest Fukien, Feng Yuan Ch'iao, im Kreise Shang-hang, 750 m., *Schindler A 19*" (*Schindler Herb.*, Berlin) may also represent this species. It was seen by the writer in 1928, but unfortunately could not be identified, as it did not match any species then known. This species evidently has a very local distribution.

Tarennia mollissima (Hook. & Arn.) Merrill in Phillip. Jour. Sci. XIII. Bot. 160 (1919).

Cupia mollissima Hooker & Arnott, Bot. Beechey Voy. 192 (1833).

Stylcoryne mollissima Benthams, Fl. Hongkong. 156 (1861).

Webera mollissima Benthams in Dunn & Tutcher, Fl. Kwangtung, 130 (1912).

Tarennia incana Diels in Notizb. Bot. Gard. Mus. Berlin, IX. 1032 (1926).—*Synon. nov.*

Tarennia vestita Diels in sched.—*Synon. nov.*

Of the species *T. incana* Diels there is available at the Arnold Arboretum not only the isotype, but also a photograph and fragments of the type. Of *T. vestita* Diels, which was apparently never published but distributed under this name, there are two collections, *H. H. Hu*, nos. 1144 and 1281, both from Kiangsi. The first species represents fruiting and the latter flowering material of the common but variable species *T. mollissima* Merrill. The characters chosen by Diels (l. c.), namely, shape at base of leaves, laxness of inflorescence, and degree of indumentum, are extremely variable; leaves showing bases that are subrotund, or obtuse, or broad-cuneate, to narrow cuneate can be found on the same branch. The rest of his description also agrees very well with *T. mollissima* Merrill.

SPECIMENS SEEN. Chekiang: Keng, 88, 243, 863; Ching 1979; Hu, 538, as *T. incana* Diels, isotype; also photo and fragment of type.—Fukien: Chung, 2236, 2316, 2828; Uong, FCU 12091.—Kiangsi: Hu, 1281 and 1144, as *T. vestita* Diels, isotype.—Kwangtung: Mell, 75, 666; Tsiang 830, 1562, 2636; Levine, 78; Chun 5561.—Hongkong: Tsiang, 652; Ford; Chun, 5097.

Viburnum Smithii Metcalf, nom. nov.

Viburnum parvifolium W. W. Smith in Notes Bot. Gard. Edinb. x. 76 (1917).—Non *V. parvifolium* Hayata.

As there is already a *Viburnum parvifolium* Hayata in Jour. Coll. Sci. Tokyo, xxx. 134 (1911) published 6 years earlier, the species described under the same name by W. W. Smith must be renamed.

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A PREVIOUSLY UNDESCRIBED VARIETY OF
LORANTHUS VITELLINUS F. v. MUELL.
FROM NORTH QUEENSLAND

W. F. BLAKELY

Loranthus vitellinus F. v. M. var. *inflata*, var. nov.

Varietas foliis coriaceis oblongo-ovatis vel ellipticis breviter petiolatis 4–6 cm. longis 2–3 cm. latis, racemis gracilibus brevibus, floribus rubris 3–6 in racemo, gemmis plus minusve lepidotis sub petalis valde inflatis.

Young parts and racemes covered with a ferruginous tomentum, as in the species. Leaves coriaceous, rather thick, oblong-ovate to elliptic, obtuse, shortly petiolate, 4–6 x 2–3 cm. Racemes slender, short, 3–6-flowered; flowers bright red, buds slightly scurfy, much inflated below the junction of the petals when fully mature.

This new variety differs from the typical form mainly in the shorter leaves and the brighter red and more inflated corolla. The latter character somewhat resembles that of *L. dictyophlebus* F. v. M.

Gadgarra Reserve, Atherton Tableland, S. F. Kajewski, no. 1163 (Arnold Arb. Exped.), July 27, 1929 (a common parasite on rain-forest trees; flowers a very pretty red, with a slight yellow ring below the stamens.)

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